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The key vigilance and behavioural predictors of looking in a group of gray-footed chacma baboons exhibiting inter-individual differences in tolerance to observers

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Contents

Abstract

In behavioural ecology, vigilance has proved a popular area of research focus over the preceding decades. Although primates have received relatively less attention than other mammals or birds, primate vigilance research has also grown considerably. In this thesis my primary aim was to identify the main drivers of vigilance use in a habituated group of gray-footed chacma baboons (*Papio ursinus griseipes*) at the Lajuma Research Centre, in the Western Soutpansberg. My review of primate vigilance literature (chapter 2) found extensive variation in terms of vigilance definition and sampling methodology that combined with other methodological inconsistency made cross-study comparisons challenging. I explored the implications of this in chapter 3 and found that different vigilance definitions can vary in their inter-observer reliability and produce varied results both within and across observers through definition and interpretation effects. Although there was no single definition that removed interpretation issues entirely, there was some evidence that more complex operationalised definitions may help remove some of the ambiguity in definitional interpretations.

Although my review of primate vigilance literature highlighted that certain themes were consistently investigated, such as the group-size effect on vigilance and sex differences, observer-effects on vigilance were largely overlooked; I therefore elected to explore habituation in the next study (chapter 4). Research on wild animals, particularly primates, has often relied upon habituation of study subjects to ensure researchers are able to observe animals directly. However, habituation is a process of declining response to a consistent stimulus as opposed to a state, and in many cases throughout behavioural ecology, it seemed to be an implicit assumption that researchers are a 'neutral' stimulus and that study subjects are 'equally' tolerant of researcher presence; however, neither factor had received much empirical attention. I explored whether these implicit assumptions had merit in the study group of baboons at Lajuma by quantifying the visual orientation distance (VOD) and flight initiation distance (FID) of all non-infant group members. The results suggested evidence of a potential personality component to the outcome of habituation processes, with individuals displaying consistent but individually distinct responses to both measures. The results of this work allowed for the extraction of individual level estimates for visual and displacement tolerance (conditional modes) that were utilised in my remaining chapters to explore the role this trait and observer proximity/behaviour had on baboon behaviour. The baboon's behavioural responses to our approaches were incredibly passive and similar to their typical responses to approaching social threats, suggesting the baboons likely considered observers as equivalent to a high-level social threat as opposed to a neutral stimulus.

During the process of assessing VODs and FIDs in the study group an adult male group member was predated by a leopard. The remaining group members exhibited an intense alarm response and gathered around the deceased animal for some time afterwards. Once this situation had begun to calm down, I assessed whether the stressful event had altered the typical VOD and FID responses of a subsample of individuals (approx. 25% of group members) during the remainder of the day (chapter 5). The individual VODs, FIDs, and individual tolerance estimates were largely unchanged, suggesting that despite the stressful event that the habituated baboons do not alter their fear perception towards researchers. FID research typically assumes that FIDs are a proxy for predation risk; however, this may not be the case if habituation processes have begun. In an increasingly urbanised world, it may become increasingly unlikely that such assumptions continue to have merit.

In chapter 6, I used focal samples collected on the baboon group between June 2018 and June 2019 to explore whether researcher proximity influenced the inter-individual proximity patterns of the habituated baboon group. I found that the interaction between individual displacement tolerance (derived from FID measures) and the distance with which I stood from a focal animal had a strong effect on how likely animals were to be neighbours of a focal animals. When I was close, the number of intolerant animals occurring as neighbours of the focal animal was lower than that of more tolerant animals this effect appeared neutralised when I was further away. Together these results suggest observers have the potential to influence the inter-individual association patterns of habituated animals, tolerance should therefore be discussed as important methodological information in these research areas, particularly studies using social network analyses.

Finally, using the looking framework I proposed for primate vigilance research in my literature review, I investigated the potential risk/vigilance drivers of looking and the specific behaviours and tasks that may constrain or promote its use in the study group at Lajuma. The risk drivers included threats posed by leopards and other groups of baboons (both preemptive and reactionary), within-group group threats, and the interaction these variables had with the baboon's physical and social environment, e.g., habitat visibility, spatial position, and group cohesion. I also used the visual tolerance estimates (from VOD assessments) to investigate how the study animals responded to observer distance and movement. My analytical approach to these questions weighted the rival hypotheses alongside one another in the same analysis and revealed that the baboons increased the duration of their looking behaviours in response to encounters with other groups and ongoing events linked with social threats (i.e., wahoo bouts and within-group conflict). Both the duration and frequency of looking bouts also had strong positive associations with the number of threatening group-members nearby. However, models exploring their specific behaviours and foraging success/items held the greatest prediction accuracy, suggesting the baboons have a propensity to utilise compatible looking time during certain behaviours and tasks, thus are likely to have up-to-date and reliable information on their threat environment at most times. In chapter 3, I also found that the baboons visually oriented towards our approaches very quickly if they were already looking around, and that this ability was not substantially hindered during engaged behaviours (e.g., digging); highlighting that the baboons were adept at detecting localised threats regardless of their behaviour. Collectively, these results suggest the study group may not need to be routinely or pre-emptively vigilant in non-threatening scenarios, and that the combination of their sensory capacity and attentiveness to their environment make them proficient at detecting threats if they are there.

Overall, this thesis highlights the importance of detecting and investigating methodological assumptions in published research, as they may not always be applicable to all study animals and groups. Within primate vigilance literature alone I found many factors that were consistently overlooked and no clear research framework to enable reliable cross-study comparisons. It may be important going forward that researchers work to consolidate methodologies at all levels to improve the comparability of results and further explore definition and interpretation effects more generally. We additionally found strong evidence that habituation may not remove the fear study animals have towards observers and therefore these topics may require additional exploration going forward. My findings highlight that it is possible to explore a range of risk and vigilance hypotheses without making habituation assumptions and without attempting to sample specific subcomponents of vigilance. Adoption of such a framework may therefore offer ways of minimising between study differences in methods without losing the ability to gather evidence supporting complex hypotheses.

Statement of copyright

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Chapter 1: Thesis introduction

1.1 Theory and methods in studying vigilance and their application to primates

Despite there being clear evidence that group-living can aid in predation avoidance, research has struggled to identify the precise mechanisms governing its evolutionary selection (1). Typically, research interested in identifying these mechanisms has explored two principle pathways: risk-dilution (2, 3) and group-vigilance hypotheses (4). The group-vigilance hypothesis, or "many-eyes effect" (5), suggests that gregariousness can be advantageous over solitary living as increasing group-size increases the likelihood that a group-member will detect a predator early and alert the remaining group-members to its location (6). It is therefore predicted that as group-size increases individual investment in vigilance should decrease, and as a result individuals can take advantage of the relative safety of groups by devoting more to time other fitness enhancing tasks, such as feeding (4, 7–9). The prediction of an inverse relationship between group-size and vigilance was initially well supported and became known as the 'group-size effect on vigilance' (10, 11).

The prediction of a group-size effect on vigilance appears to have been born out of the model presented by Pulliam (4); however, its simplicity has been criticised (1), as it overlooks whether individual risk is always uniform across groups (9) and numerous other confounding factors including (but not limited to) food density, foraging intensity, competition, sex, age, and dominance (10). As a result, there have been ongoing attempts to incorporate additional factors into model frameworks, such as cheating (12), risk of starvation, confusion, and benefits of direct detection over group detection (8). More recently, computational frameworks have allowed the costs and benefits of grouping behaviours to be incorporated (13) whilst controlling for the confounding factors highlighted by other authors (9, 10). However, the inclusion of additional factors necessitates numerous assumptions: 1) Vigilance is always functioning to detect predators, 2) Vigilance is always costly, or incompatible with feeding behaviours (i.e., a foraging-vigilance trade-off), and 3) Individual vigilance is more effective than collective vigilance. In addition, the framework of Olson *et al* (13) contains assumptions that group members always perceive actual group-size, and group members always communicate predator sightings to the rest of the group. These are all bold assumptions that are not universally justified (1).

Exploration into group-size effects on vigilance have been important in research on primates as many species live in groups. As Treves (14) highlighted however, an increasing number of studies (particularly on primates) had not reported a group-size effect on vigilance. Treves hypothesized that primate groups contained a mix of age-sex classes and vulnerable or non-vulnerable individuals, such that risk is not uniform across group members. Therefore, the group-size effect on vigilance is unlikely to be explained by risk-dilution in larger groups (9).

It has also been highlighted that many species of primate are able to feed upright and use their hands to gather or manipulate food, potentially lessening the impact of the foraging-vigilance trade-off discussed in many other taxa (15). If foraging and vigilance are not mutually exclusive activities, then a group-size effect on vigilance may not be expected (16). Despite this, feeding has been associated with lower vigilance than other behaviours in *Cebus* monkeys (17) but empirical data concerning the sensory capacity of primates during different behaviours is lacking (14). To complicate matters further, vigilance use may also be influenced by an interaction between food items (or foraging substrate) and the current foraging success of the focal animal. For example, animals in a high-quality food patch may forgo vigilance to maximise food intake. Alternatively, an animal may forgo long vigilance-bouts during complex foraging tasks and instead rely on frequent or infrequent glances to collect information on threats (14).

A more popular hypothesis to explain the absence of a group-size effect on vigilance in primates is the conspecific risk hypothesis, that as group-size increases, so too does the risk of engaging in conflict with another group-member, i.e., a positive group-size effect on vigilance would be predicted (14). Early vigilance research typically only considered the function of vigilance to be predator detection (4, 12) but a growing body of work has accumulated evidence that group-living animals and primates in particular, utilise social or within-group vigilance (1, 14, 18, 19). These competing hypotheses pose a complex problem for researchers to disentangle analytically when no attempts are made to sample antipredator and social vigilance separately. In these scenarios, comparisons between smaller and larger groups may not detect vigilance differences as diminished investment in antipredator vigilance may be offset by animals monitoring their conspecific threats more often (14).

An alternative method has emerged whereby researchers have attempted to define and sample the specific subcomponents of vigilance. For example researchers have sampled social monitoring specifically to explore foraging and competition hypotheses (20), whilst social monitoring and antipredator vigilance have been recorded distinctly to elucidate the competing group-size hypotheses (21). Another popular distinction is between occasions when animals routinely or pre-emptively scan for potential threats versus induced or reactionary vigilance (e.g., (22–24)). The former describes active visual search of the environment by an animal, in the absence of threatening stimuli, whilst reactionary or induced vigilance is the visual response of an animal to the detection of a threatening stimulus. Accurately sampling reactionary forms of vigilance is likely to be intuitive in most scenarios involving predation threats (i.e., presence/absence of a predator) and during intense encounters with foreign individuals/groups (19, 25, 26); however, the behavioural differences between preemptive and reactionary vigilance for within-group threats may be challenging to detect. It is also unclear if we should anticipate preemptive vigilance for predators to have different behavioural markers than preemptive vigilance for within-group threats, and equally, whether vigilance is always distinguishable for other forms of looking (1, 27). Despite these being clear issues, few studies have formally noted whether they are exploring preemptive or reactionary vigilance, whilst the concept of these subcomponents has generally been overlooked in most studies.

Perhaps unsurprisingly, subtle differences in definition have emerged throughout primate vigilance studies. For example, “subject looked up towards the sky” (28), and “Lifting of the head, breaking eye contact with food, during foraging” (29) both allow for vigilance to be multifunctional, but the contexts in which it is recorded are different. Rose & Fedigan’s (30) definition of vigilance “Intently staring beyond immediate vegetation with a stationary, alert posture”, does not necessarily exclude any vigilance function; however, the requirement of an “alert posture” constrains when vigilance can be recorded, whilst “intently staring” introduces ambiguity, asking observers to interpret the behaviour of the focal animal. This variation poses a problem; if definitions of behaviours are subtly different, the information researchers collect may also be different, making comparisons between studies challenging. Nevertheless, despite briefly discussing methodological variation it was rejected as a potential reason for varying results within primate vigilance research (14), although a formal assessment has not been conducted.

The Oxford Dictionary (31) defines vigilance as “The action or state of keeping careful watch for possible danger or difficulties”. Beauchamp (1), in a review of animal vigilance literature, put forward a biological definition, viewing vigilance as the behaviour or state of “monitoring the surroundings for potential threats”. Interestingly, both definitions suggest the sole function of vigilance is to detect threats or difficulties. This idea is not a new one, Galton (32) wrote: “The protective senses of each individual who chooses to live in companionship are multiplied by a large factor, and he thereby receives a maximum of security at a minimum cost of restlessness”. This highlights that the antipredator benefits of group-living have been speculated for some time; however, vigilance definitions seldom use behavioural markers exclusively associated with threat detection and monitoring (1).

Devising vigilance definitions that flawlessly capture when an animal is in a state of monitoring its surroundings for threats and difficulties is undoubtedly challenging and fraught with subjectivity issues (1). An animal may raise its head to pre-emptively search for predators or within-group threats, but it may also raise its head to search for food or travel paths. There is not yet a clear consensus on whether all of these stimuli reflect vigilance use, which may have led to a range of perspectives emerging (1). It has been suggested that vigilance can function as a more general behaviour of looking, with vigilance used to collect information on a variety of different stimuli (33). Therefore, vigilance could serve numerous functions, including personal food search (34), monitoring of threatening group-members (18, 35), intra- and inter-sexual competition (36, 37), gestures between individuals (38, 39), movement and navigation (14, 40), and scanning for prey (41, 42). However, allowing vigilance to serve so many functions would necessitate redefining the word itself, as not all of the aforementioned stimuli are associated with danger, threats, or difficulties as defined by (1, 31).

In chapter 2 of this thesis (43), I review several sources of methodological variation in primate vigilance research in a more in-depth and systematic manner. This review highlights that there appears to be no clear perspective on defining vigilance, especially in primate research, and little work addressing the advantages and disadvantages of certain ethoses and perspectives. In addition, despite Treves (14) rejecting that methodological inconsistencies could have driven the varied results found within primate vigilance literature, there has been a rapid growth in primate vigilance research since the last review on the subject. As such, methodological variation has also grown, yet no research has explored the implications of this variation empirically. Without a clear consensus on the specific role of vigilance nor consolidation onto similar methods for defining and sampling its use, it becomes very challenging to disentangle common trends across the primate order. In chapter 2, I offer a potential solution to these issues by suggesting researchers adopt a more general looking framework. In chapter 3, I explore the implications of definitional variation and investigate whether certain definitions (including the looking framework) are more prone to inter-observer differences in interpretation than others.

As it is ultimately very challenging to understand the internal state of an animal, it is unlikely that any definition will flawlessly detect an internal state of vigilance in any animal. General definitions, such as the looking framework I proposed, or the definition presented by Treves (44) (“scanning directed beyond an arm’s reach”) offer a potential workaround for these issues but they make a very bold assumption - that any form of looking/scanning behaviour in which an animal focuses beyond an arm’s reach (or the individual/item/substrate its hands are in contact with) should detect a predator if it is present, regardless of whether the animal is vigilant or not. This essentially speculates that animals can collect multiple types of information concurrently, or in other words, that different information acquisition pathways are compatible. Although this is highly likely for many species of primate, such a definition does not directly and specifically sample vigilance as defined by (1, 31), and requires empirical evidence to ensure the validity of these assumptions. In chapter 4, as part of a broader study exploring habituation using flight initiation distance methods, I explore the detective capacity of the study group during different behaviours and postures and investigate the compatibility of the baboon’s general looking behaviours with threat detection.

Despite methodological variation, primate vigilance research has explored a wide variety of potential drivers of vigilance including factors relating to the focal animals themselves, revealing that age-sex class and dominance status also influence vigilance patterns (23, 45–50). The influence of female reproductive state has also received attention (24, 44, 51, 52) as has maternal factors such as infant proximity (51, 53, 54). The role of the focal animal's social environment on vigilance use has been very popular, with a variety of approaches reported including the effect number of neighbouring conspecifics/group cohesion (17, 18, 44, 52, 55–59), age-sex class/identity/rank of neighours (17, 30, 52), the relationship between focal animals and their neighbours (18, 19, 25, 60).

A host of environmental and ecological variables are also likely to influence an individual's perception of risk and as such, primate vigilance research has explored how vigilance patterns are varied according to differences in foliage density, habitat structure and visibility (19, 57, 58, 61–63). Vigilance is consistently reported to decrease with height in canopy for a number of species (17–19, 23, 25, 46, 52, 64); however, across all these cases, differences in sampling design have made cross-study comparisons challenging. For example, some studies use a ground/above ground dichotomy (46), whilst others utilize categorical distinctions for increasing height with variable category sizes (e.g., 0-1 meters (18), 0-3 meters (58), 2-5 meters (17)). Spatial position (17, 44, 52, 65–67), habitat exposure (17, 45), distance from refuge (57, 63), areas of range overlap with other groups (25, 30, 52), and home-range boundary areas (59) have also been explored.

Despite a plethora of factors receiving thorough attention thus far, some areas have received relatively less attention or have been overlooked entirely. One consistent assumption is that habituated animals view observers as neutral stimuli and as such, it has been mostly overlooked whether observers can influence an animal's behaviour during direct observations. Additionally, little work has explored how habitat modification, anthropogenic disturbance (68), and human-shield effects (69) can influence vigilance patterns in wild primate groups. In captive scenarios, the role of habituation and inter-observer effects is less of a concern, especially as experiments can be designed to remove the stimulus posed by observers (70–72); however, this is not possible when direct observations are used on wild habituated animals. Attempts to record and exclude looks towards observers have been made (73, 74), but only one study has retained vigilance data in which the focal animal has directed vigilance towards observers and then used this data to explore whether observers may be a potential driver of vigilance use (25). Thus, the role observers have in influencing the behaviours they record remains a glaring gap in primate vigilance research and potentially animal behaviour research more generally. As there is potential for animals to vary in their tolerances of researchers, I explore whether it is possible to quantify these factors in individual animals and use this data to individual behavioural patterns, such as looking or vigilance.

1.2 Habituation and tolerance in research using direct observations

Habituation has been referred to as "a process that leads to decreased responsiveness to a stimulus" (75), or as a "behavioural response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue" (76). The opposite process, known as sensitization, is when an individual becomes more responsive to a stimulus (75). At any moment in an organism's life the current outcomes of these processes (to a range of stimuli) can be referred to as tolerance, a state reflecting an individual's prior experiences with a particular stimuli, highlighting that tolerance can fall anywhere on the habituation/sensitization spectrum at any point in time (75).

In primate behavioural research, habituation processes have been used to reduce the fear wild primates have towards human observers. This reduced fear perception allows researchers to undertake direct observations under the assumption that study subjects view them as a neutral stimuli (77). The plethora of research articles using direct observations of habituated subjects suggest this outcome has been formally tested; however, little research has explored observer neutrality explicitly. In addition, it remains unclear if the outcome of habituation processes (i.e., tolerance) is equal across all individuals, groups, populations, and species. Given the lack of research focusing on observer neutrality and equal tolerance outcomes, there is a possibility that both are implicit assumptions that have become a methodological orthodoxy in animal behaviour research using direct observations.

If the assumption that all individuals, groups, or species are equally habituated is not valid then behaviours such as vigilance or looking could be at risk of being sampled in a biased manner. In addition, research focusing on facets such as proximity relationships, could also be challenging to sample accurately if animals with different tolerance levels tend to associate, e.g., a highly intolerant individual may often associate with another individual sharing the opposite trait (i.e., highly tolerant), if the presence of observers displaces intolerant individuals, then the aforementioned proximity relationship may be challenging to sample robustly. Furthermore, an individual may alter its typical patterns of space use to avoid proximity with observers (78), leading to unnatural spatial patterns (e.g., cohesion) emerging within a group. The key issue is that if subtle variation in individual tolerance levels is missed, then a potential driver of the observed behavioural patterns is unaccounted for.

Thus far the many interacting variables that influence the habituation process have been well-studied in primatology (79); whilst several behaviours have been found to decrease during habituation processes, including observer-directed aggression (80) and self-directed behaviours (81). Remote sensing technology has also been used to explore the effect of human-observer presence on the behaviour of habituated white-faced capuchins (*Cebus capucinus*), but Crofoot et al (82) found no evidence that activity patterns, ranging behaviour, or proximity to neighbouring conspecific groups were influenced by the presence of observers. Although the presence/absence of observers is clearly an important avenue for future research, it does not explore the individual tolerance outcomes (of habituation processes) and thus does not offer an effective paradigm for understanding the real-time implication of observer presence on animal behaviour nor aid in quantifying differences in tolerance between individuals, groups, or species.

Thus far, assessments of the outcomes of habituation processes (i.e., tolerance) has often been based on qualitative assessments of behaviour. For example, “full habituation” was described as “individual accepts humans (and apparently ignores them) at close range during all activities; they appear calm when they are alone with humans and are relatively easy to follow while travelling” (83). These forms of assessment are subjective, prone to inter-observer reliability issues, and fail to detect subtle differences that may exist between individuals, groups or species. As a result, research has failed to produce quantitative data that would allow comparisons across different groups, species, or individuals.

In chapter 4, I utilise protocols developed by flight initiation distance researchers to quantify the visual and displacement distances of each study animal. FID methods require a researcher to approach a focal animal and record the distance at which the animal visual orients towards and displaces away from the approaching researcher (84), and therefore offers a viable and ecologically valid method for quantifying individual tolerances towards researchers (see (85)). However, flight initiation distance (hereafter FID) research has thus far highlighted a vast range of factors that can determine the response of focal animals to researcher approaches. Thus, these hypotheses required thorough investigation in order to understand tolerance phenomena effectively.

1.3 Using FID methodology to explore tolerance

Optimal escape theory predicts that the distance at which animals decide to flee from an approaching threat (i.e., FID), is determined by a trade-off between the risk of being injured or killed and the benefits of staying to engage in any fitness enhancing activity (86–89), essentially predicting that increasing risk should correlate with increased FID (87, 90). Predation threats are typically explored in most FID research, but measuring a true FID (in response to an actual predator) is unlikely, although this has been achieved under lab-experimental conditions (91, 92). As a result, studies concerning FID and escape behaviour have commonly used approaching human-observers to measure FID instead. This methodological approach is considered valid in most species as humans are often considered predators by these animals (93). This has enabled the use of human approaches (in FID methodology) to become a consistent method for assessing perceived predation risk, as it apparently reflects the aforementioned fitness cost-benefit conundrum for animals (88, 94–96).

A vast body of work now supports that FID increases with increasing risk in a variety of prey species for a range of extrinsic "risk" factors, including speed of approach (97–99), directness of approach (99–101), and distance from refuge or cover (102–105). Intrinsic factors relating specifically to the individual being approached have found better body condition associated with longer FID in Balearic lizards (*Podarcis lilfordi*) (106), and body size often reported to have a positive relationship with FID (98, 104). Broader environmental level factors have also been shown to influence FID including habitat type (107), habitat protection status (104), habitat or site specific human exposure levels (105), whilst biogeographical factors such as insularity have also yielded strong effects (98, 108). Factors relating to the social environment of group-living animals have received less attention, although group-size was reported to explain significant variation in FID in great egrets (*Ardea alba*) and western sandpipers (*Calidris mauri*) (109) but group-size was not a key determining factor in the FID responses of 83 birds species investigated by (110).

FID research has also investigated a host of variables related to the approaching observer (pseudo-predator). For example, starting distance is one of the most widely reported factors influencing FID (103, 105, 107, 109–111), although may be the result of methodological biases as opposed to a true biological effect (112). The direction of attention (of approaching observer) has also been shown to influence FID (97), whilst observer identity has also been implicated, and therefore it is often recommended that future FID research should limit all approaches to a single observer (84). Although this would make analytical aspects easier to design and interpret, it would likely limit the understanding of observer effects going forward as comparisons wouldn't be possible. Januchowski-Hartley, Nash, & Lawton (113) detected differences in mean FID responses between three observers; however, this effect was not considered statistically robust, and therefore concluded there was no evidence of observer bias. In addition, the effect of observer attire (e.g., dive gear), and equipment (e.g., carrying spear gun) was not found to influence FID estimates. Predator size has also been implicated (108, 114), whilst Guay et (115) found observer differences in detection distance (see below) suggesting research must be careful to either control for the stimulus or identity of approachers, or alternatively make this element an integral part of their study design.

FID approach methodology also affords researchers the opportunity to record and explore additional variables. In particular detection distance, often termed alert distance has been recorded as the distance focal animals detect or become vigilant of approaching observers (84). This has allowed two other measures to be calculated: detection delay (distance between start point and detection) and assessment time/interval (distance between detection point and FID) (116). An additional factor, neighbour flight distance, could also be recorded in gregarious species but research has yet to explore it. The flush early and avoid the rush (F.E.A.R) hypothesis (117), which suggests that animals that detect approaching threats earlier should flee earlier to avoid the costs of monitoring approaching threats, has been tested using both detection distance and assessment interval. A meta-analysis across three taxonomic groups revealed general support for the F.E.A.R hypothesis (96), whilst additional empirical work has also provided support for roe deer (*Capreolus capreolus*) (116), and 61 of 75 bird species evaluated by (118).

The F.E.A.R hypothesis is not necessarily dependent upon observers being considered equivalent to predators, and therefore is an important research avenue for tolerance related questions. For example, if an individual, species, or group tends to be visually sensitive to the movement of observers, this will result in rapid detection. Rapid detection, particularly at longer distances, evokes attentional costs for study subjects, such as monitoring the observer instead of engaging in fitness enhancing tasks. Therefore, as detection distance increases, the monitoring costs increase as study subjects dedicate more time to monitoring the observer. In these scenarios study subjects can readily and easily avoid these costs by displacing sooner and thus fulfil the predictions of the F.E.A.R hypothesis (a strong positive relationship between FID and detection interval) (117). If, however, intolerant individuals were to consistently displace rapidly after detection regardless of distance, whilst tolerant individuals exhibit consistent or repeatable FID regardless of detection distance, it would render F.E.A.R a poor predictor of flight behaviour, and support notions that study subjects are not ‘equally’ tolerant of researchers.

Individual repeatability is a common assumption found within FID research (e.g., (94)) but has received relatively less attention that other factors. Consistent individual differences in FID were not found in yellow-bellied marmots (*Marmota flaviventris*) (111), although more recent work on the same species concluded that FID was repeatable in yearlings (119). Several species reportedly exhibit strong individual repeatability in FID, including burrowing owls (*Atene cunicularia*; (120, 121)), barn swallows (*Hirundo rustica*; (122)), Namibian rock agamas (*Agama planiceps;* (123)), striped plateau lizards (*Sceloporus virgatus*; (88)), and male reindeer (*Rangifer tarandus;* (124)). A lack of repeatability often infers that some degree flight or detection distances are driven by environmental factors (e.g., predation risk or F.E.A.R); however, if a factor such as trial number is the key predictor, researchers have often inferred that study subjects underwent habituation or sensitization processes to the approach methods, e.g., individual FID decreases with successive trials suggesting habituation to FID methods.

Interestingly, two of the studies exploring individual repeatability in FID have been conducted within a personality paradigm, with both studies using FID as a proxy for measuring boldness (119, 123). This approach relies upon the assumption that human-approachers are considered threatening or novel. Carter et al (123) makes no mention of Namibian rock agamas receiving consistent human-disturbance or habituation attempts, suggesting that in this case the assumption was likely valid, despite not being explicitly tested. Petelle et al (119), however, highlight differential anthropogenic disturbance distributed across their study colonies of *M.flaviventris.* The authors accounted for this by averaging human-traffic at two locations and assigning the higher value to four of seven colonies (which received higher anthropogenic disturbance) and the lower value to the remaining three colonies. These values were included as predictors in multivariate analysis revealing that FID decreased (i.e., boldness increased) with increased pedestrian traffic for both yearlings and adults. This suggests consistent anthropogenic disturbance may have contributed to an ongoing habituation process in four out of the seven study colonies at this field site. As a result, study subjects may have no longer considered human-approachers as high-level threats.

This literature therefore suggested that in order to isolate the key drivers of the baboon's visual orientation and flight responses, I would need to measure numerous methodological (e.g., start distance, trial number, researcher identity), environmental (habitat type, height), social (neighbour flee first, number of neighbours, ongoing risky events), and behavioural (e.g., looking or not looking, engaged or not engaged in a task such as foraging or grooming) variables during approaches. In chapter 4, I present a study that investigates these hypotheses in detail. In addition, I retained individual identity in model analyses to understand within individual consistencies and between individual differences. If the baboons displayed consistent but individually distinct responses to FID approaches through time and across and range of scenarios, there would be strong evidence to suggest that tolerance varies between individuals, i.e., they are not equally 'habituated'. This design also enabled the behavioural responses of the baboons (e.g., passive displacement) to be recorded, allowing insights into the threat perception the study group have towards researchers. The outcomes of such analyses also enabled the extraction of conditional modes (individual tolerance estimates), which were used as covariates in subsequent studies (chapters 6 and 7) to understand the impact researchers have on study subject's behaviours.

1.4 Baboons

The gray-footed chacma (*Papio ursinus griseipes* (Pocock, 1911) is a large bodied, diurnal, and terrestrial animal belonging to the *Cercopithecidae* family within the Primate Order. Although the *Papio* genus is widely spread across the African continent, with hamadryas baboons also found within part of the Arabian Peninsula, *Papio ursinus* is located primarily within southern Africa with *P. u. griseipes* found mainly in northern South Africa and southern Zambia (125). *Papio* species are considered highly sexually dimorphic; however, juvenile males and females are generally similar sizes until around 3 years of age, after which males experience rapid musculoskeletal growth compared to females (126). Chacma baboons typically live in large multi-male, multi-female groups, with group sizes as low as 4 (127) to 6 (38) individuals and above 100 (128).

Female baboons typically remain in their natal groups for their entire lives, larger groups composed of numerous matrilineal subgroups or 'families' arranged in linear dominance hierarchies, i.e., the females in one matrilineal group outrank all the individuals in the subordinate matriline (129). Dominant females often direct threats and aggressions towards subordinate females (129), and although this structure is typically stable, i.e., females do not compete for position, female rank instability has been observed (130). Although males will often transfer groups at some stage, some do choose to remain in their natal group, with a high degree of social affiliation potentially disincentivising the emigration decision in some cases (131). In cases where males do immigrate into other groups, they can often become highly aggressive and there are usually infanticide risks (130, 132). Unlike the female group members, male baboons are often engaged in agonistic competition for rank positions, leading to ongoing dominance instability. It is often challenging to infer precise rankings as the most aggressive individuals do not always dominate every dyadic encounter (133).

1.5 Study site and baboons at Lajuma

I conducted this study on a single group of habituated chacma baboons at the Lajuma research centre in the western Soutpansberg Mountains, Limpopo Province, South Africa (central coordinates: 23°06'45.14"S 29°11'37.10"E) (see figure 1). The study site is made up of numerous different habitat types, which has produced a high level of biodiversity in the area (134). As a result, the area contains several predator species known to prey on baboons, including leopard (*Panthera pardus*), crowned eagle (*Stephanoaetus coronatus*), and rock python (*Sebae natalensis*) and research on leopard diets has shown that baboons are an important component of leopard diets in the study area (135, 136). Although leopards are thought to preferentially target adult baboons, baboons are also known to aggressively defend and mob leopards (137), making predatory attempts highly risky for leopards. Aggressive defensive is observed in most interactions between the baboons at Lajuma and leopards (personal observations). Three successful predations by leopards have been observed since 2015, highlighting leopards are a key threat to this baboon group. Unlike adult baboons, juvenile baboons are also at risk from a variety of other predators, including rock python and crowned eagle, with the study group at Lajuma also displaying both avoidance and aggressive behaviours towards both species on several occasions. An attempted predation by a rock python on a juvenile baboon resulted in the study group attacking and fatally wounding the python, although the group recovered the juvenile baboon it died shortly after (*Personal communication: Pete Tomlin*).

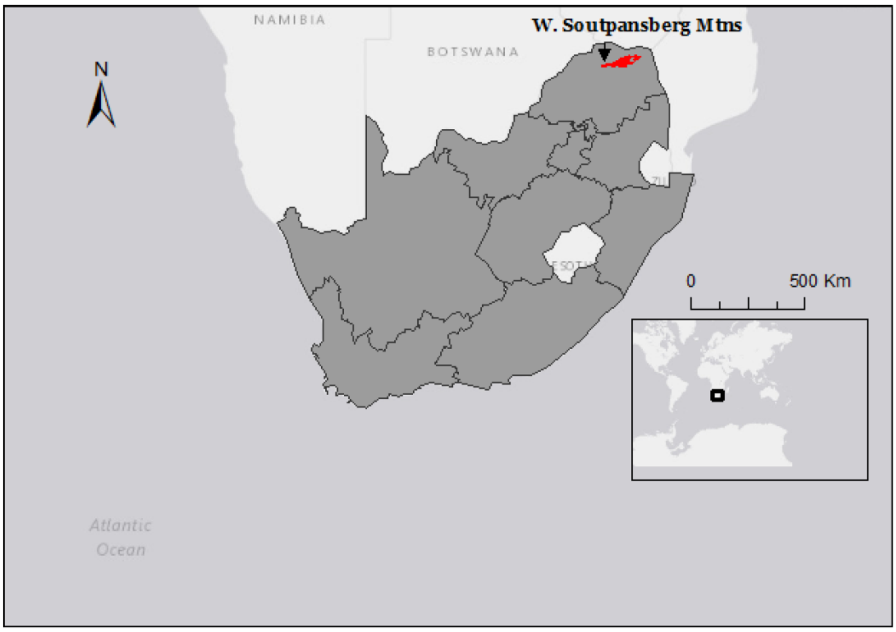

Figure 1. Image highlighting the location of the Soutpansberg Mountain (red) in South Africa (grey), with the arrow indicating the western portion of the mountain range where Lajuma Research Centre is located (138).

In most chacma baboon populations, several groups' home-ranges overlap, with interactions between groups ranging from passive to aggressive (139, 140). Although baboons are not known for exhibiting territoriality, some groups have been observed aggressively defending the edges of their home-ranges from competing groups (141). I estimated there to be at least 6 other groups of baboons at Lajuma that the study group came into contact with across different parts of their range. Reactions to the presence of foreign individuals and groups could range from passive to group-wide alarms including chasing and fighting, suggesting that the study group are likely wary of threats posed by these other groups. One notable factor is that most of these study groups were unhabituated; as such, the outcome of interactions between groups were likely influenced by our presence to some degree. Regardless, the risk posed by inter-group encounters could form an important component of the study group's behavioural patterns (138, 142).

This baboon study group have previously formed the basis of theses by Louise de-Raad (2012), Caroline Howlett (2012), Peter Tomlin (2016), and Alec Ayers (2019). During the period I studied the group, the group grew from approximately 76 individuals (during drought conditions 2015/16) to 92 individuals by July 2019 (see table 1). For the duration of the PhD research, I was able to identity every individual including infants. Although, emigration and immigration of adult and adolescent male baboons presented as commonplace in baboon research, both appeared less common by comparison in the habituated group at Lajuma. During the 4.5-year period only 3 adult males transferred into the group permanently, whilst numerous individuals remained with their natal group well into maturity. Nevertheless, frequent agonistic behaviours were still prevalent in the group, suggesting within-group social risks were still high. The study group's ranging patterns consistently take it outside of the Lajuma property and onto several other properties, which range in management practices and levels and type of human interactions. The land-use practices on these properties have occasionally led to negative interactions between humans and baboons. As a result, the baboons seem to view humans as a risk on certain properties, although this does not appear to affect their tolerances towards researchers.

Table 1. Summary information for the size of the study group and totals for each age-sex class at the start of each year. Observations were completed in July 2019; thus, information is given for the conclusion of the study period.

Year	Infant females	Infant males	Juvenile females	Juvenile males	Adolescent females	Adolescent males	Adult females	Adult males	Total
2015	2	3	17	23	2	2	22	5	76
2016	2	1	16	24	3	2	24	6	78
2017	3	5	14	20	6	4	23	8	83
2018	5	7	11	20	4	3	22	8	80
2019	4	8	15	25	5	2	24	8	91
July - 2019	7	6	15	25	4	2	25	8	92

1.6 Thesis aims

The following thesis is broken down into 6 chapters exploring the following aims:

1. How can we study primate vigilance effectively? (Chapters 2, 3, and 7)
   a. What results have been found so far?
   b. What methods have been used in vigilance research?
   c. What are the consequences of methodological variation?
   d. Is there a solution to methodological variation?
2. To understand whether the implicit assumptions of direct observations on habituated animals are valid in the habituated study group (Chapter 4).
   a. Are observers considered a neutral stimulus by the study animals?
   b. Are all animals habituated equally?
   c. If not, can we quantify their tolerance levels for further research?
3. What are the outcomes of inter-individual tolerance differences? (Chapters 5, 6, and 7)
   a. Do observers influence inter-individual associations patterns?
   b. Is tolerance consistent even during highly threatening events?
   c. Do observers influence visual behaviours, e.g., looking or vigilance?
4. What are the key scenarios predicting changes in looking patterns in chacma baboons? (Chapters 3, 4, and 7)
   a. Is there evidence that they interrupt their current behaviours to pre-emptively monitor their environment for threats?
   b. Or do they rely on reactive vigilance more often?
   c. Is there evidence they can collect multiple types of information concurrently?

d. Do certain behaviours and tasks promote or constrain looking behaviours to different extents?

Chapter 2. Primate vigilance research

What have we been looking at? A call for consistency in studies of primate vigilance

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What have we been looking at? A call for consistency in studies of primate vigilance

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Abstract

Vigilance functions to detect threats. In primates, these threats emerge from both predators and conspecifics, but a host of other social, demographic, and ecological factors have been shown to influence primate vigilance patterns. The primate vigilance literature is thus characterized by considerable variation in findings, with inconsistent or contradictory results reported not only across different species but also within species and populations across studies. Some of this variation could emerge from fundamental differences in the methods employed, making comparisons across species and groups challenging. Furthermore, identifying consistent behavioral markers for the state of vigilance appears to have proved challenging in primates, leading to a range of definitions being developed. Deviation at this level leads directly into concomitant variation at the level of sampling methodologies. As a result, the primate vigilance literature currently presents a diverse series of approaches to exploring subtly different behaviors and phenomena. This review calls for a greater consistency in studying vigilance, with the aim of encouraging future research to follow similar principles leading to more comparable results. Identifying whether an animal is in a vigilant state is challenging for most field researchers; identifying and recording a more general behavior of "looking" should though be more achievable. Experimental approaches could then be employed to understand the compatibility "looking" has with predator detection (and other threats) in individual study systems. The outcome of this approach will allow researchers to understand the key determinants of looking in their study groups and explore threat detection probabilities given an individual or group's relative level of looking.

KEYWORDS
conspecific threats, dominance, glances, predator detection, scanning

1 | INTRODUCTION

Group-living is widespread throughout the animal kingdom, with most adaptive explanations centering on its antipredator benefits. Early explanations for grouping suggested that that animals benefited from forming aggregations as it decreased individual risk of predation (Bates, 1863; Belt, 1874). Despite there being clear evidence that group-living or aggregation formation can aid in predation avoidance, research has struggled to identify the precise mechanisms governing its evolutionary selection (Beauchamp, 2015). Typically, research interested in these mechanisms has explored two principle pathways, namely risk-dilution (Hamilton, 1971; Vine, 1971) and the group-vigilance hypotheses (Pulliam, 1973).

The group-vigilance hypothesis, otherwise known as the "many-eyes effect" (Powell, 1974) or "collective detection" (Lima, 1995), suggests that gregariousness carries the advantage of cumulative senses, increasing the likelihood of early detection of predators (Miller, 1922). As group size increases, therefore, the level of vigilance performed by individual group members should decrease. Reduction in individual vigilance allows animals to take advantage of the relative safety of groups by devoting more time to other fitness enhancing tasks such as foraging (Bednekoff & Lima, 1998; Dehm, 1990; McNamara & Houston, 1992; Pulliam, 1973; Roberts, 1996). The prediction of an inverse relationship between group size and vigilance was initially well supported, and became known as the "group-size effect on vigilance" (Elgar, 1989; Lima, 1995). Interestingly, however, an increasing number of studies, particularly on primates, do not report a group-size effect on vigilance (Treves, 2000).

Treves (2000) explored possible explanations for this lack of consistent support for the group-size effect in primates, focusing on

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several assumptions consistently made about predator and prey species. For example, one specific assumption was the idea of a trade-off between vigilance and feeding, or put another way, the assumption that vigilance and feeding were incompatible. Primates can feed upright or use their hands to harvest and manipulate food, potentially allowing them to handle food and scan concurrently (Cowlishaw et al., 2004). However, Treves (2000) found no evidence that this explained the lack of support for a group-size effect on vigilance in primates, instead concluding that the absence of a group-size effect may be partially accounted for by within-group vigilance. Certainly, vigilance has been reported to be important in mate and competitor detection in male chacma baboons (*Papio ursinus*) (Cowlishaw, 1998), in social monitoring for within-group threats in chimpanzees (*Pan troglodytes schweinfurthii*) (Kutsukake, 2006), and monitoring both within-group and extra-group threats in blue monkeys (*Cercopithecus mitis*) (Gaynor & Cords, 2012). Furthermore, group size may hold a low predictive value for individual predation risk, since groups contain a mix of age-sex classes and vulnerable and non-vulnerable individuals (Treves, 2000). Indeed, with a plethora of confounding variables influencing individual risk of predation, the group-size effect on vigilance is unlikely to be explained by risk-dilution in larger groups (Roberts, 1996).

At the end of his influential review, Treves (2000) concluded that several functional differences in vigilance behavior and safety in groups accounted for primates deviating from the group-size effect. Nearly two decades on, however, what emerges is that the group-size effect is just one area where the literature of primate vigilance paints a picture of inconsistent or variable results. Over the same period, it has become evident that a variety of other social, demographic, and ecological factors could also play a role in shaping primate vigilance patterns. To bring things up to date, therefore, we first review the factors influencing primate vigilance. This highlights an important finding; the primate vigilance literature is characterized by a large number of apparently contradictory studies. Although some of this may be expected given the diversity of visual systems, social systems and ecological pressures across species, contradictory results are also apparent within species. We propose that part of this variation may be explained by the considerable methodological inconsistencies that have emerged between studies. Interestingly, primate studies were significantly underrepresented in the theoretical chapters in a recent comprehensive review of the vigilance literature (Beauchamp, 2015), despite representing a significant proportion of the available studies. To some extent this is likely to reflect the factors we identify to account for the variation in primate vigilance research that undermines the comparability of studies. Nevertheless, the importance of primate study systems for addressing questions relating to social threats is probably underappreciated. We thus present a framework for future studies of primate vigilance behavior.

2 | VARIATION IN PRIMATE VIGILANCE STUDIES

We conducted an extensive literature review that identified 59 studies exploring vigilance in (non-human) primates (Supporting Information Table S1—study list), 27 of which have been conducted since Treves' (2000) review. Studies span the wild and captivity, although understandably focus on haplorrhines given the inherent challenges of studying vigilance in nocturnal species (Beauchamp, 2015). Within the haplorrhines, New World monkeys, Old World monkeys, and apes were all well represented. Studies have explored vigilance in relation to a broad range of topics including group size, nearest neighbors, social dynamics, spatial position and vegetation structure or density (Table 1). Studies of many of these factors have led to inconsistent findings.

Group size effects remain a significant area of focus. Although some studies have reported evidence for vigilance declining with group size (de Ruiter, 1986; Isbell & Young, 1993), many find no effect (Treves, 2000). For example, Treves, Drescher, and Ingrisano. (2001) failed to detect a group-size effect on vigilance in black howler monkeys (*Alouatta pigra*). Some studies, however, have isolated a group-size effect by exploring specific behavioral and socio-ecological conditions. Hill and Cowlishaw (2002) reported that adult female chacma baboons in smaller groups spent more of their foraging time vigilant, once refuge proximity, habitat type and neighbor proximity had been controlled for. Stojan-Dolar and Heymann (2010) initially found no evidence of a group-size effect in single species groups of mustached tamarins (*Saguinus mystax*), likely due to unusually large study groups. Nevertheless, a negative group-size effect was present when *S. mystax* formed mixed species groups with saddleback tamarins (*Saguinus fuscicollis*), although this effect was only apparent during resting behaviors. When Gosselin-Ildari and Koenig (2012) defined "antipredatory vigilance" and "social monitoring" as separate behaviors, they subsequently detected a negative group-size effect on "antipredatory vigilance" in common marmosets (*Callithrix jacchus*). Similarly, when vigilance of this species was categorized as either "induced" or "routine", the frequency of "induced vigilance" (scans longer than 1 s) increased with group size (Teichroeb & Sicotte, 2012).

Alongside these group size phenomena, factors such as distance to nearest neighbors and number of neighbors in close proximity have been shown to influence primate vigilance patterns. Studies have consistently reported vigilance to decrease when focal animals had at least one neighbor(Steenbeek, Piek, van Buul, & van Hooff, 1999; Stojan-Dolar & Heymann, 2010; Treves, 1998; Treves et al., 2001; van Schaik & van Noordwijk, 1989), whilst increased time spent alone (Rose & Fedigan, 1995) and decreased density of nearby neighbors (relative to distant neighbors) (Treves, 1999b) increase individual vigilance use. Despite both Kutsukake (2006) and Watson et al. (2015) reporting that number of neighbors did not significantly affect vigilance in chimpanzees and rhesus macaques (*Macaca mulatta*) respectively, a host of other studies have shown vigilance use to decrease with increasing number of neighbors (Busia, Schaffner, & Aureli, 2016; Cowlishaw, 1998; Stojan-Dolar & Heymann, 2010), although sometimes only for specific behaviors (Stojan-Dolar & Heymann, 2010; Teichroeb & Sicotte, 2012). Robinson (1981) found that wedge-capped capuchins (*Cebus olivaceus*) increased vigilance with increasing distance to nearest neighbor; conversely, Suzuki and Sugiura (2011) reported vigilance increased as distance to nearest group member decreased in Japanese macaque (*Macaca fuscata*) adult females.

TABLE 1 Sample of reported effects in studies of primate vigilance patterns highlighting variability in published relationships

Factor	Effect	References
Sex	Males more vigilant	Baldellou & Henzi (1992), Busia et al. (2016), de Ruiter (1986), Fragaszy (1990), Gould et al. (1997), Isbell & Young (1993), Rose & Fedigan (1995), Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)[a], Treves (1998, 1999c), van Schaik & van Noordwijk (1989), Watson et al. (2015)
	No difference between sexes	Cowlishaw (1998), Gould (1996), Gould et al. (1997), Macintosh & Sicotte (2009), Smith, Kelez & Buchanan-Smith (2004), Teichroeb & Sicotte (2012), Treves (1998)
Dominance	Subordinates more vigilant than dominants	Alberts (1994)[b], Caine & Marra (1988), Gaynor & Cords (2012), Haude et al. (1976), Keverne et al. (1978), Pannozzo et al. (2007)
	High-ranking individuals more vigilant	Alberts (1994)[c], Gould (1996), Gould et al. (1997), Isbell & Young (1993), Rose & Fedigan (1995), Watson et al. (2015)
	No effect of rank	Robinson (1981)
Adult females with Infants	Mothers with dependent infants more vigilant than those with independent young or females without infants	Boinski et al. (2003), Treves (1999c), Treves et al. (2003)
	No difference found between adult females with or without infants	Treves (1998)
	All adult individuals increased vigilance after birth of infants	Treves et al. (2001)
	Vigilance increased when infant-carrying	Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)
Age	Vigilance increases with age in both sexes	Boinski et al. (2003), Busia et al. (2016), de Ruiter (1986), Fragaszy (1990), Gosselin-Ildari & Koenig (2012)
	Vigilance decreased with age in both sexes	Watson et al. (2015)
	No age-related effects	Caine & Marra (1988)
Activity	Vigilance higher during resting and traveling	van Schaik & van Noordwijk (1989)
	Vigilance higher during resting	Cowlishaw (1998), Gaynor & Cords (2012), Stojan-Dolar & Heymann (2010), Suzuki & Sigiura (2011)
	Vigilance lower during grooming than resting or feeding	Cords (1995)
	Routine vigilance higher during feeding	Teichroeb & Sicotte (2012)
	No difference between feeding or resting	Macintosh & Sicotte (2009), Teichroeb & Sicotte (2012)
	Vigilance higher during foraging than resting	Kutsukake (2006)[d]
	Vigilance lower during foraging than resting	Kutsukake (2006)[e]
	Vigilance lowest during grooming	Stojan-Dolar & Heymann (2010)
Group-size	No group-size effect	Cowlishaw (1998), Rose & Fedigan (1995), Stojan-Dolar & Heymann (2010), Treves (1998), Treves et al. (2001)
	Positive group-size effect	Gosselin-Ildari & Koenig (2012)[f], Stojan-Dolar & Heymann (2010)[g], Teichroeb & Sicotte (2012)[g]
	Negative group-size effect	de Ruiter (1986), Gosselin-Ildari & Koenig (2012), Isbell & Young (1993), Kazahari & Agetsuma (2010)[f], Hill & Cowlishaw (2002)[h]
Subgroup size	Vigilance lower with larger subgroup sizes but only in boundary areas	Busia et al. (2016)
	No effect of daily party size	Kutsukake (2006)
Group composition	Vigilance rate higher in single-species groups	Chapman & Chapman (1996), Cords (1990)
	Species composition did not influence vigilance	Chapman & Chapman (1996), Treves (1999a,c)
	Individual vigilance rate lower in larger mixed-species groups	Chapman & Chapman (1996), Hardie & Buchanan-Smith, (1997)

(Continues)

TABLE 1 (Continued)

Factor	Effect	References
Spatial position in group	Increased vigilance when peripheral	Robinson (1981), Steenbeek et al. (1999), Treves (1998), van Schaik & van Noordwijk (1989)
	No effect of spatial position on vigilance	Hall & Fedigan (1997), Josephs et al. (2016), Treves (1998)
Number of neighbors	Vigilance decreases with increasing neighbors	Busia et al. (2016), Cowlishaw (1998), Gaynor & Cords (2012)[i], Rose & Fedigan (1995), Stojan-Dolar & Heymann (2010), Teichroeb & Sicotte (2012)
	Vigilance lower with at least one adult neighbor	Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010), Treves (1998), Treves et al. (2001), van Schaik & van Noordwijk (1989)
	Vigilance increases with increasing neighbors	Kutsukake (2006, 2007)
	No significant effect	Kutsukake (2006), Watson et al. (2015)
Distance to neighbors	Vigilance increased as distance to nearest group member decreased	Suzuki & Sigiura (2011)
	Vigilance increased as distance to nearest conspecific or heterospecific neighbor increased	Robinson (1981), Stojan-Dolar & Heymann (2010)
	Vigilance higher with few neighbors near and many neighbors farther away, and vice versa.	Treves (1999b)
Sex of neighbor	Vigilance lower when one or more adult male neighbors	van Schaik & van Noordwijk (1989)
	Vigilance increases with increasing male neighbors	Rose & Fedigan (1995)
	Adult female's greater vigilance towards male neighbors	Dunbar (1983), Watts (1998)
	Adult females with infants less vigilant with adult male present	Steenbeek et al. (1999)
	No effect of adult male presence	Steenbeek et al. (1999)
Rank of neighbors	Vigilance greater towards dominant animals	Gaynor & Cords (2012), McNelis & Boatright-Horowitz (1998)
	Proximity of alpha male had no influence on vigilance	de Ruiter (1986)
Relationship to neighbor	Affiliative neighbors increase vigilance	Dunbar (1983), Watts (1998)
	Vigilance increases with non-affiliative individuals	Kutsukake (2006)
	Agonistic neighbors relationships increase vigilance	Keverne et al. (1978), Pannozzo et al. (2007), Watts (1998)
Foliage density	Vigilance declines with increasing foliage density	Cords (1990), Cowlishaw (1998)[e], Gaynor & Cords (2012)
	No significant effect of habitat visibility	Alberts (1994), Hill & Cowlishaw (2002), Stojan-Dolar & Heymann (2010)
Height in canopy	Decrease with height in canopy	de Ruiter (1986), Gaynor & Cords (2012), Hirsch (2002), Kutsukake (2006), Macintosh & Sicotte (2009), Smith, Kelez & Buchanan-Smith (2004), Teichroeb & Sicotte (2012), van Schaik & van Noordwijk (1989)
	Most vigilant near the ground	Campos & Fedigan (2014)
Distance from refuge/exposed	Lower vigilance when exposed	van Schaik & van Noordwijk (1989)
	Increase vigilance with distance from refuge or when exposed	Baldellou & Henzi (1992)[e], Cowlishaw (1998), Hill & Cowlishaw (2002)[h], Josephs et al. (2016), van Schaik & van Noordwijk (1989)
Landscape of fear	Vigilance increased in higher risk areas	Campos & Fedigan (2014)

(Continues)

TABLE 1 (Continued)

Factor	Effect	References
Range overlap	More vigilant in areas of range overlap	Macintosh & Sicotte (2009), Steenbeek et al. (1999), Rose & Fedigan (1995)
	No effect	Steenbeek et al. (1999)
Home-range boundary areas	Higher vigilance in areas close to the boundary of the home-range	Busia et al. (2016)

[a]Males more vigilant at one site with higher male to female ratio. [b]Daughters of low- versus high-ranked mothers. [c]Sons of low- versus high-ranked mothers. [d]Males only. [e]Females only. [f]Social monitoring only. [g]Resting only. [h]Foraging or feeding only. [i]Only when neighbors are kin.

Age-sex class, identity, and rank of neighbors are also key determinants of vigilance use in a range of primate species. When one or more neighbors were adult, male vigilance was lower in both white-fronted capuchins (*Cebus albifrons*) and tufted capuchins (*Cebus apella*) (van Schaik & van Noordwijk, 1989) whilst similar effects were reported for Thomas's langurs (*Presbytis thomasi*), but only in adult females with infants (Steenbeek et al., 1999). Opposite effects were found for white-faced capuchins (*Cebus capucinus*); however, with vigilance increasing with increasing number of male neighbors (Rose & Fedigan, 1995). Vigilance has also been shown to increase based on the relationship between focal individuals and neighbors. For example, vigilance increased in adult female blue monkeys when either of the two highest-ranking females were nearby (Gaynor & Cords, 2012), when individual mountain gorilla (*Gorilla gorilla beringei*) who share agonistic relationships were in proximity (Watts, 1998), and when non-affiliates were in proximity (Kutsukake, 2006). Vigilance in ursine colobus (*Colobus vellerosus*) was lower in presence of familiar versus unfamiliar neighbors (MacIntosh & Sicotte, 2009).

Factors relating to focal animals, such as their age-sex class and dominance status also influence vigilance patterns (Chance, 1967), with numerous studies reporting males to be more vigilant than other age-sex classes (Baldellou & Henzi, 1992; de Ruiter, 1986; Fragaszy, 1990; Gould, Fedigan, & Rose, 1997; Isbell & Young, 1993; Rose & Fedigan, 1995; Steenbeek et al., 1999; Treves, 1998, 1999c; van Schaik & van Noordwijk, 1989; Watson et al., 2015). Nevertheless, a number of other studies report no difference between sexes (Cowlishaw, 1998; Gould, 1996; Gould et al., 1997; MacIntosh & Sicotte, 2009; Teichroeb & Sicotte, 2012; Treves, 1998). Subordinate individuals have been reported as being more vigilant than dominants in several species (Chance, 1967; Caine & Marra, 1988; Gaynor & Cords, 2012; Keverne, Leonard, Scruton, & Young, 1978; Pannozzo, Phillips, Haas, & Mintz, 2007); conversely, however, high-ranking individuals are found to be more vigilant in other species (Gould et al., 1997; Isbell & Young, 1993; Watson et al., 2015). Alberts (1994) found daughters of low-ranking yellow baboon (*Papio cynocephalus*) mothers glanced more often than daughters of high-ranking mothers, whilst sons of high-ranking mothers glanced more often than their low-ranking counterparts. Rose & Fedigan (1995) found that alpha male white-faced capuchins tended to be the most vigilant individual in each group, whilst Gould (1996) reported a similar result for alpha female ring tailed lemurs (*Lemur catta*), but found no relationship between vigilance behavior and dominance rank among adult males. Interestingly, two studies on rhesus macaques have produced opposite results, with Haude, Graber, and Farres. (1976) reporting that subordinates are more vigilant than dominants, whilst Watson et al. (2015) reported that high-ranking individuals were more vigilant, although Haude et al (1976) also notes that intermediates in the dominance hierarchy were the most vigilant individuals.

When "social monitoring" has been recorded as a distinct behavior, varied results have emerged with Gosselin-ildari and Koenig (2012) reporting social monitoring to increase with group size, whilst Kazahari and Agetsuma (2010) found social monitoring frequency was higher in small feeding groups of Japanese macaques. The subject of gaze may also be important. Female gelada (*Theropithecus gelada*) were found to glance significantly more at males than other females in their unit and also tended to glance more frequently at regular grooming partners than other females, regardless of rank. In addition, glance rates of males towards females were most strongly correlated with female rank, although the result was not significant (Dunbar, 1983). In captive talapoin monkeys (*Miopithecus talapoin*), dominants paid more attention to the opposite sex compared with subordinates. Adult female eastern gorillas were more likely to cease feeding and focus on males than females (Watts, 1998), whilst lower ranking patas monkeys (*Erythrocebus patas*) gazed toward higher-ranking animals more often than vice versa (McNelis & Boatright-Horowitz, 1998). These studies serve to highlight the importance of social vigilance in primates, despite the inconsistent patterns reported, supporting to some extent the classic predictions of Chance (1967) on "attention" in primate groups.

The effect may extend to extra-group social monitoring. Vigilance was found to increase in areas of range overlap with other groups in both ursine colobus (MacIntosh & Sicotte, 2009) and Thomas's langurs, although this latter effect was not consistent across all conditions (Steenbeek et al. 1999). Rose and Fedigan (1995) reported that male white-faced capuchins in two of the three groups with overlapping ranges were more vigilant in areas of overlap. Similarly, higher vigilance in areas close to the boundary of the home range has been reported in black-handed spider monkeys (*Ateles geoffroyi*) (Busia et al. 2016).

Investigations into the influence of reproductive state of adult females on vigilance have also yielded variable results. Despite Treves (1998) reporting that there was no difference in vigilance use between adult females with or without infants in both redtail monkeys (*Cercopithecus ascanius schidtii*) and red colobus (*Procolobus badius tephroceles*), several subsequent studies reported that mothers with dependent infants more vigilant than those with independent young or females without infants (Boinski et al., 2003; Steenbeek et al., 1999; Treves, 1999c; Treves, Drescher, & Snowdon, 2003). It has also been reported that all adult individuals increased vigilance after birth of infants in black howler monkeys (Treves et al., 2001), and vigilance increased during infant-carrying in mustached tamarins (Stojan-Dolar & Heymann, 2010). When infants are separated from their mothers, mothers increase vigilance if the infants are out of their mother's reach, but not when moving alone (Onishi & Nakamichi, 2011). Treves (1999c) also found that females glance towards other conspecifics more frequently when infants are younger or out of contact. Treves et al. (2003) highlighted that the greatest increase in vigilance was found when immatures were conspicuous; however, allogrooming has been shown to reduce maternal vigilance towards infants in several species (Kutsukake, 2006, 2007; Maestripieri, 1993; Treves, 1999c). Finally, Gosselin-Ildari & Koenig (2012) reported that "antipredatory" vigilance was higher for breeding than non-breeding individuals, whilst "social monitoring" was mostly unaffected by breeding status.

Beyond exploring social, reproductive and demographic determinants of vigilance, the effect of a range of ecological factors has also been investigated. Vigilance rate has been shown to reduce with increasing foliage density in redtail monkeys and blue monkeys (Cords, 1990; Gaynor & Cords, 2012), but habitat structure and visibility had no effect on vigilance in yellow baboons (Alberts, 1994), chacma baboons (Hill & Cowlishaw, 2002), and mustached tamarins (Stojan-Dolar & Heymann, 2010). However, Stojan-Dolar and Heymann (2010) found that vigilance was highest in medium density vegetation during passive grooming, whilst male vigilance was reportedly higher in open than closed habitats in chacma baboons (Cowlishaw, 1998). Vigilance is consistently reported to decrease with height in canopy for a number of species (de Ruiter, 1986; Gaynor & Cords, 2012; Kutsukake, 2006; MacIntosh & Sicotte, 2009; Smith, Kelez, & Buchanan-Smith, 2004; Steenbeek et al., 1999; Teichroeb & Sicotte, 2012; van Schaik & van Noordwijk, 1989) although de Ruiter (1986) noted that vigilance was lowest on the ground for wedge-capped capuchins. Conversely, Kutsukake (2006) reported vigilance was highest at 0–1 m in chimpanzees while white-faced capuchins which were also reportedly most vigilant near the ground (Campos & Fedigan, 2014). Stojan-Dolar and Heymann (2010) found that vigilance initially decreased within increasing height in *S. mystax* but increased again at higher canopy levels.

Higher levels of vigilance have been reported in animals occupying exposed positions (Baldellou & Henzi, 1992; van Schaik & van Noordwijk, 1989). Josephs Josephs, Bonnell, Dostie, Barrett, and Peter Henzi (2016) reported the same effect when using spatial position as a proxy for exposure in vervet monkeys (*Chlorocebus pygerythrus*) but white-faced capuchins were reported to exhibit lower vigilance when exposed (van Schaik & van Noordwijk, 1989). Cowlishaw (1998) reported that chacma baboons in Namibia increased vigilance with distance from refuge; when data from this population was combined with those of a single group from a South African population, the same effect was found but only during foraging behaviors (Hill & Cowlishaw, 2002). Increased vigilance has also been reported in spatially peripheral individuals (Robinson, 1981; Steenbeek et al., 1999; Treves, 1998; van Schaik & van Noordwijk, 1989), although no effect of spatial position on vigilance has been reported in other species (Hall & Fedigan, 1997; Treves, 1998). White-faced capuchin vigilance behavior was heightened in higher risk areas in the absence of actual threats (Campos & Fedigan, 2014).

2.1 | Variation in primate vigilance studies: What's the problem?

Considerable variation exists across and within primate species in the relationships between vigilance and its social, demographic and ecological drivers. Of course, many of these results could reflect the actual differences that exist within and across different primate groups. Nevertheless, whilst several potential determinants of primate vigilance have received widespread investigation (e.g., age-sex class, number of neighbors), there is considerable variation in approaches and the environmental and social factors explored as predictor variables. Indeed, this variation is indicative of more fundamental variation that exists within the methodological approaches used in primate vigilance. Interestingly, this was a topic briefly touched on by Treves (2000), who highlighted that many primate studies use idiosyncratic sampling rules and definitions of vigilance. He concluded, however, that methodological differences could not account for the absence of a group-size effect on vigilance and instead focused on functional explanations for why we expect a group-size effect on vigilance (Treves, 2000). Nevertheless, given the greater diversity of primate vigilance research now available it seems pertinent to revisit this vital area, since the variation in methodological approaches appears to be of much greater significance that envisaged at that time. In particular, the two key methodological levels in which primate vigilance studies show inconsistency appear to have been critically important:

1. Variation in how vigilance is defined.
2. Variation in sampling methodology.

Although both facets are clearly important for interpreting research into primate vigilance, a key issue is that variation at one level directly feeds into all other aspects of the study. As a result, variation at either level could make it challenging to compare studies, and so make it difficult to determine whether new or inconsistent findings are specific to primates in general, species, or study groups. Robust sampling methodologies are critical of course, but we initially explore the historical use of the term vigilance in animal studies, as this may help to understand the variation that exists within primate vigilance literature.

3 | VIGILANCE TERMINOLOGY AND INTERPRETATIONS OF BEHAVIORS

Although Belt (1874) suggested that animals benefit from being in groups because it is unlikely an approaching threat would go undetected by all group members, the first published work that discusses the idea of predator detection in terms of sensory capacity appears to be Galton's (1871) study of Damara cattle. Even so, while the terms "glance" and "alert" appear, "vigilance" isn't explicitly mentioned. Galton instead describes that Damara cattle can use the senses associated with eyes, ears and nose to monitor the environment for threats.

Over a decade later, Oswald (1885) discussed the notion that as monkeys face predation risk during dark hours, they can alleviate risk via the increased vigilance use of group members acting as sentries. This appears to be the first use of the term vigilance in this context, although Holder (1885) used the terms “vigilance”, “vigilant”, and “watchfulness” when describing the aggressive nest guarding behavior of male four-spined sticklebacks (*Apeltes quadracus*). Moving forward, further studies began to use the term vigilance in a range of contexts, although a formal definition was lacking (Cameron, 1908; Davis, 1941; Hartley, 1947; Williams, 1903), whilst other studies continued to discuss vigilance with regards to threat or predator detection without making reference to the actual term vigilance (Jenkins, 1944; Leopold, 1951; Marler, 1956).

Much early research used a range of terms that are generally considered anthropomorphic now, such as guarding or sentry, and their use is now generally avoided (Beauchamp, 2015). Hall (1960) was critical of terms such as “sentinel” when used to describe the behaviors of male chacma baboons, suggesting they were presumptive and should be discarded in favor of more objective observations. Nevertheless, he used the term “watchfulness” to describe lengthy periods where individuals appeared to have elevated vigilance, suggesting that during these periods the individuals were either “nervous”, “restless”, or “irritable”. Thus, despite the valid call for greater objectivity, Hall (1960) appears to have drawn conclusions based on subjective assessments of the state of the animals.

The next major leap forward appears to center on Pulliam’s (1973) model exploring how the probability of detecting a predator increases with group size. Pulliam assumed that “head-cocks” were used by birds to detect predators, and that individual birds could diminish investment in this behavior as group size increased without succumbing to increased predation risk. Despite being widely cited in studies of animal vigilance, the term “vigilance” wasn’t used a single time in the article, instead “head cocks” by flock members were assumed to place the individual group members in a posture allowing them to collect information on predation threats. This highlights some of the underlying assumptions of this model; that certain behaviors or postures adopted by an animal completely close off other information acquisition pathways, assuming incompatibility between the head-down posture (i.e., foraging) and predator detection.

Postural terms that simply document the behavior of an animal, such as “looking-up” (Jenkins, 1944), “head-cocks” (Pulliam, 1973), “raising-head” or “head-turning” (Marler, 1956) seem on the surface to be an adequate method for recording animal vigilance. However, definitions of the term vigilance suggest more precise requirements: “The action or state of keeping careful watch for possible danger or difficulties” (Oxford Dictionary, 2017). Beauchamp (2015), in a large-scale review of animal vigilance literature, put forward a definition from a biological perspective, viewing vigilance as the behavior or state of “monitoring the surroundings for potential threats”. Interestingly, both definitions suggest the sole function of vigilance is to detect threats or difficulties; such requirements are unlikely to be captured by postural definitions alone. The key problem, therefore, is how to detect when an animal is actually in a vigilant state? Researchers typically attempt to identify a postural change or behavioral response made by a study animal that shows they are in a vigilant state. Beauchamp (2015) refers to these outward behavioral signs as “markers” for vigilance. The aim when identifying a good marker for vigilance is that it should be consistently performed concurrent to an animal being in a vigilant state, and be almost never observed when not in a vigilant state. Such conditions are challenging to fulfill.

Most markers of vigilance cannot claim to be the true “markers” Beauchamp (2015) describes, since animals could use “head cocks” (Pulliam, 1973) or “head-up” (Cowlishaw, 1998) to collect multiple forms of visual information that are not all related to threats. For example, “raising of the head” or “scanning the environment” could also be used in personal food search (Giraldeau & Caraco, 2000; Treves, 2000), monitoring of threatening group-members (Hall, 1960; Kutsukake, 2006), intra- and inter-sexual competition (Burger & Gochfeld, 1988; Jenkins, 1944), gestures between individuals (Hall, 1962; Hausfater & Takacs, 1987), movement and navigation (Mueller, Fagan, & Grimm, 2011; Treves, 2000), and scanning for prey (Cameron, 1908; Hartley, 1947).

Dimond and Lazarus (1974) presented an alternative definition of vigilance from an operations research perspective, with vigilance being “a measure of the probability that an animal will detect a given stimulus at a given instant in time”. More vigilant individuals then have a higher probability of detecting a stimulus or event. This seems to be the first use of the term vigilance to describe the collection of multiple types of information; in this sense vigilance is not exclusively linked to detecting predators but instead, as the behavior of “looking”, allowing an individual to be attentive to multiple sources of information. This definition enables the consideration of intraspecific competition as a function of vigilance, whilst also allowing for vigilance to be used to collect information on other non-threatening stimulus, such as resources. However, this definition would require the term vigilance to be redefined to incorporate all forms of visual information acquisition, regardless of whether the visual stimuli are threatening or not.

Although it is possible that an animal in a vigilant state can also collect a range of additional information simultaneously, vigilance is rarely considered a multifunctional looking behavior. Instead definitions typically present vigilance as a subset of looking behaviors associated with threat detection. This does not, however, reduce the problems associated with identifying true “markers” for vigilance in animals. In fact, it seems likely that sampling vigilance is a challenging goal for certain taxa, particularly primate species. Indeed, several studies have now gone a step further and subcategorized their study species looking behaviors into different types of vigilance (e.g., routine or induced vigilance: Blanchard & Fritz, 2007). Such classifications also have important implications for how we design our studies.

3.1 | Types of vigilance

Definitions of vigilance tend to identify it as a precautionary or preventative behavior, functioning to assess risk at given moment in time, allowing for early detection of threats. Once a threat has been detected, however, an animal could also use vigilance to monitor that threat, and so inform an animal's evasive behaviors and decision to flee (Beauchamp, 2015). Such distinctions are evident in studies that have separated vigilance into "routine" and "induced" components (Blanchard & Fritz, 2007; Teichroeb & Sicotte, 2012). Routine vigilance concerns an animal's visual monitoring behaviors during its "spare time", suggesting that no threatening stimuli are present. In contrast, induced vigilance concerns the active response to a stimulus. Vigilance has also been subdivided into "preemptive" and "reactionary" terms (Boinski et al., 2003); pre-emptive vigilance requires active visual search of the environment by an animal in the absence of threatening stimuli. Reactionary vigilance on the other hand is the visual response of an animal to the detection of a threatening stimulus. Similar classifications have been used to define "anti-predator" vigilance (Hirsch, 2002) and vigilance "towards a potential predator" (Gould, 1996).

Although the terminology used by these studies varies, they point to similar distinctions within vigilance behavior. One important implication is that "reactive" vigilance is recorded whenever an observer detects a threatening stimuli (Blanchard & Fritz, 2007; Boinski et al., 2003; Gould, 1996; Hirsch, 2002; Teichroeb & Sicotte, 2012), or alternatively when an observer notices a behavioral change in members of the study group that betrays the presence of a threat (e.g., blatant evasive behaviors: Boinski et al., 2003). Although the distinction between preemptive and reactionary vigilance is intuitive with regards to predation threats, monitoring social threats is likely to be more nuanced and the distinction between preemptive and reactionary vigilance therefore more challenging. Although reactive vigilance should be possible to record during encounters between rival conspecific groups (Gaynor & Cords, 2012; Gould, 1996; MacIntosh & Sicotte, 2009), within-group vigilance is unlikely to produce behavioral changes that are as simple to detect. As a consequence it may be challenging to robustly separate these forms of vigilance in primate groups where social threats are also prevalent. To counteract this, authors have tried to tease apart anti-predatory vigilance and social vigilance, although the distinction between "social vigilance" (Jack, 2001) or "within-group surveillance" (Treves, 1999c) and anti-predator vigilance is challenging (Beauchamp, 2015). Identifying true markers for these distinct vigilance behaviors may be unachievable. Perhaps unsurprisingly, therefore, primate studies have adopted a diversity of vigilance definitions. Few, however, have formally noted whether they are exploring preemptive or reactionary vigilance; however, and this issue has generally been overlooked in most studies.

3.2 | Primate vigilance definitions

All primate vigilance studies have provided vigilance definitions in describing their methods and this reveals significant variation in how the behavior of vigilance is defined. Some definitions require an interpretation of an animal's "state", others utilize visual terminology (e.g., looking, gazing, staring, etc.), or require a head or eye movement, while operational definitions that treat vigilance as a multifunctional behavior have also been proposed. Many definitions incorporate a number of these facets. This diversity is encapsulated by the plethora of interchangeable terms used within primate vigilance studies (Table 2; Supporting Information Table S1).

Some definitions require an interpretation of an animal's state (Table 2). For example, Campos and Fedigan's (2014) definition of "scanning intently at long range while alert and stationary" imposes a requirement of an animal being "alert" so constraining when vigilance can be recorded, whilst "scanning intently" necessitates an interpretation the behavior of the focal animal. This type of definition appears to be a clear attempt to identify a "marker" for vigilance, but the need for observers to interpret an animal's state from a postural or behavior change may not be objective, particularly when they are not naïve to the questions of study. Terms such as "cautiously observing" (de Ruiter, 1986) or scanning/staring "intently" (Gould et al., 1997; Rose & Fedigan, 1995) add a further complexity to similar definitions in the literature; both contain adverbs that ask observers to make an interpretation of an animal's current behavior.

The use of a visual term to define a vigilance term is common practice in primate vigilance literature (Table 2). Terms such as "gaze", "attention", "scanning" or even "looking" carry similar problems to the definitions based on an individual's state; they do not necessarily infer a state of vigilance but instead ask observers to interpret when an animal is collecting visual information. The key problem in this instance is that each term is open to interpretation. Several different observers could potentially converge on a similar theoretical understanding of what "gaze" means, but could interpret the act of "gazing" differently to one another when recording data in their study. Objective definitions of this sort are challenging.

Numerous studies appear to try and tackle this problem by using postural changes or eye movement in elements of their vigilance definitions (Table 2). Some of these definitions take a very concise multifunctional form such as "head up, eyes open" (Cowlishaw, 1998) or "movement of the head and/or eyes" (Gaynor & Cords, 2012), whilst other authors have added postural requirements to vigilance definitions such as "lifting of the head" (Caine & Marra, 1988) or "turning the head" (Suzuki & Sugiura, 2011). Some are more precise such as "Raising and lowering of the line of vision by at least 30 degrees relative to the horizontal plane" (Bshary & Noe, 1997), or "Head movement of at least 45°, in any direction" (Steenbeek et al., 1999). Although these definitions could potentially alleviate issues concerning interpreting the internal state an animal or the objectivity of visual terms, consistently estimating these angles of movement accurately may be difficult for animals that regularly change orientation in the horizontal and vertical planes. It has also been highlighted by Treves (2000) that primates often feed in an upright sitting position, or alternatively can feed in a range of tripedal and bipedal postures, each of which would have their own sensory limitations. Cowlishaw et al. (2004) have shown that upright posture use concurrent to food handling can allow animals to use vigilance; head movement may thus not be necessary to adopt a vigilant state.

Because primate vigilance studies have shown continued interest in the supposed trade-offs between foraging and vigilance this has led to vigilance only being recorded during foraging and stationary behaviors (Table 3). Recording vigilance in moving animals is challenging, and

TABLE 2 Selection of terms and key behavioral requirements used in vigilance definitions in the primate vigilance literature

Key behavioral requirements	Term	References
Actively searching	Preemptive vigilance	Boinski et al. (2003)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004)
Alert and stationary	Vigilance	Baldellou & Henzi (1992), Campos & Fedigan (2014), Gould et al. (1997), Rose & Fedigan (1995),
	Non-social vigilance	Jack (2001)
Cautiously observing	Scanning	de Ruiter (1986)
Eyes open	Vigilant	Cowlishaw (1998), Hill & Cowlishaw (2002)
Eye movement	Glances	Dunbar (1983), Keverne et al. (1978), Maestripieri (1993)
	Looking up/down	Bshary & Noë (1997)
	Scan	Cowlishaw et al. (2004)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004)
	Vigilant scanning	Gaynor & Cords (2012)
Gazing	Glance and Look	Watts (1998)
	Vigilance	Kutsukake (2006, 2007)
	Scanning	Isbell & Young (1993)
Head up	Vigilant	Cowlishaw (1998), Hardie & Buchanan-Smith (1997), Hill & Cowlishaw (2002), Kutsukake (2006, 2007), Robinson (1981), van Schaik & van Noordwijk (1989)
Head movement	Glances	Alberts (1994), Keverne et al. (1978), Maestripieri (1993)
	Looking/Look-up	Bshary & Noë (1997), Caine & Marra (1988), Hardie & Buchanan-Smith (1997), Watson et al. (2015)
	Routine/induced scans	Teichroeb & Sicotte (2012)
	Scanning	Caine (1984), Cowlishaw et al. (2004), de Ruiter (1986), Fragaszy (1990), Hardie & Buchanan-Smith (1997), Koenig (1998), Macintosh & Sicotte (2009), Suzuki & Sigiura (2011)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004), Steenbeek et al. (1999), Stojan-Dolar & Heymann (2010)
	Vigilant scanning	Gaynor & Cords (2012)
Look	Vigilance	Robinson (1981) van Schaik & van Noordwijk (1989)
	Anti-predatory vigilance	Gosselin-Ildari & Koenig (2012)
	Social monitoring	Gosselin-Ildari & Koenig (2012)
Scanning/staring intently	Vigilant	Campos & Fedigan (2014), Gould et al. (1997), Rose & Fedigan (1995)
	Look up	Hardie & Buchanan-Smith (1997)
	Preemptive vigilance	Boinski et al. (2003)
Scanning the environment	Vigilant	Baldellou & Henzi (1992), Gould (1996), Gould et al. (1997), Koenig (1998)
	Social monitoring	Kazahari & Agetsuma (2010)
	Scanning	Tsingalia & Rowell (1984)

several studies have excluded sampling vigilance use during travel activities, or when focal animals move beyond a certain distance during observations (Gaynor & Cords, 2012; Smith et al., 2004; Stojan-Dolar & Heymann, 2010; Treves, 1998, 1999a; Treves et al., 2001). Although such definitions can help methodologically by restricting the focus of data collection it nevertheless limits the understanding of vigilance and questions that can be addressed with the data.

Problems surrounding postural definitions appear to have been circumnavigated via the development of multifunctional vigilance definitions, which operationalize vigilance based on excluding behaviors that are likely inhibit its use. In a series of articles on several different primate species, Treves consistently defined vigilance as any visual search or scanning "directed beyond an arm's reach" (see Treves, 1998, 1999a, 1999b, 1999c, 2000, Treves et al., 2001, 2003). This definition

TABLE 3 Selection of studies that restrict observations to certain activities or exclude vigilance use during specific behaviors

Behavior required or excluded	Term	References
Restricted vigilance records to:		
During water drinking only	Looking bouts	Watson et al. (2015)
Feeding	Vigilance: Scans/Glances	Cords (1990)
	Glances	Dunbar (1983)
Foraging	Looking	Caine & Marra (1988)
	Scan	Cowlishaw et al. (2003)
Feeding or foraging	Glance/Look	Watts (1998)
Feeding or resting	Vigilant scanning	Gaynor & Cords (2012)
	Scanning	Treves (1999c)
Feeding or moving	Glances	Alberts (1994)
Feeding, resting, grooming	Look-ups	Cords (1995)
Feeding, travelling, resting, grooming	Vigilant	Cowlishaw (1998)
Slow-moving or stationary	Scanning	Treves et al. (2001), Treves et al. (2003)
Stationary	Anti-predatory vigilance	Gosselin-Ildari & Koenig (2012)
	Vigilance toward a potential predator or unknown source	Gould (1996)
	Visual scanning	Koenig (1998)
	Vigilance	Smith, Kelez & Buchanan-Smith (2004), Stojan-Dolar & Heymann (2010)
Stationary sitting posture	Vigilance	Kutsukake (2006, 2007)
Stationary or moving	Scan	Fragaszy (1990)
Excluded observations when:		
Animal moved >10 m	Scanning	Treves (1998, 1999a), Treves et al. (2001), Treves et al. (2003)
Grooming	Non-social target (look), Social target (look)	Pannozzo et al. (2007)
Social activities	Vigilant	van Schaik & van Noordwijk (1989)

highlighted that "Scanning serves many purposes (food search, travel-path planning, etc.), but an animal searching for food may incidentally spot a predator" (Treves, 1999b). This bears direct resemblance to the operational definition of vigilance provided by Dimond and Lazarus (1974). Despite not explicitly stating that the definitions utilized are concerned with either preemptive or reactionary vigilance, Treves consistently made it clear that he was recording vigilance as a multifunctional looking behavior, suggesting that any form of looking would be recorded, without forming a prior expectation of the information an animal was collecting. The work of Treves (Treves, 1998, 1999a, 1999b, 1999c, 2000, Treves et al., 2001, 2003) appeared to popularize these ideas, with several recent studies citing this work as justification for a multifunctional vigilance definition (Busia et al., 2016; Gaynor & Cords, 2012; Stojan-Dolar & Heymann, 2010). Earlier authors had also arrived at similar definitions. Chapman & Chapman (1996) required the animal "looked up, away from the substrate it was on, or away from the food item it was processing", while van Schaik and van Noordwijk (1989) defined vigilance as "Looked around, providing it was not inspecting vegetation or partners at close range". Hall and Fedigan (1997) defined vigilance as scanning areas and substrates not in an animal's immediate proximity (within 3 m), while definitions requiring animals to look outside their immediate vicinity or substrate have appeared in a number of studies (Baldellou & Henzi, 1992; Gould et al., 1997; Hirsch, 2002; Jack, 2001; Josephs et al., 2016; Rose & Fedigan, 1995). Provided the immediate vicinity is objective and defined, these definitions should be easier to replicate across studies. In doing so it may obviate many of the problems of using a "marker" approach to recording vigilance.

Although multifunctional definitions remove many of the problems associated with inferring the state of vigilance in an animal or defining the significance of head movements, one implication is that researchers are technically no longer studying vigilance per se, but are instead focused on the behavior of "looking". As a result, a divergence has emerged within the literature, with the most recent work suggesting authors are trending towards the use of multifunctional definitions. This is likely a robust course of action to take provided researchers

TABLE 4 Time requirements attached to terms within vigilance definitions in primate studies

Time requirement	Term	References
<1 s	Routine scans	Teichroeb & Sicotte (2012)
"Up to about 1 s"	Glance	Watts (1998)
>1 s	Induced scans	Teichroeb & Sicotte (2012)
	Look	Watts (1998)
	Watch	Watts (1998)
<2 s	Glance	Cords (1990)
≥2 s	Scans	Cords (1990)
>3 s	Visual scanning	Suzuki & Sigiura (2011)
5 s or less	Glances	Alberts (1994)
"Fast" <5 s	Aerial/Terrestrial Glance	Barros et al. (2008), Nunes et al. (2010)
"Long-lasting" ≥5 s	Aerial/Terrestrial Scan	Barros et al. (2008), Nunes et al. (2010)
≥10 s	Visual scanning	Caine (1984)
	Vigilance	Caine (1987)
"At least for a short period" (an entire 5-s interval)	Visual scanning	Koenig (1998)
Uninterrupted for at least 5 s	Anti-predatory vigilance	Gosselin-Ildari & Koenig (2012)
"Any length of time"	Look	McNelis & Boatright-Horowitz (1998)

bear in mind that multifunctional approaches do not explicitly explore vigilance patterns.

One final important element of the definitions of vigilance concerns the lack of consistency in the use of terminology. For example, what constitutes a "glance" in one study may not constitute a "glance" in another. Understandably, many authors have attempted to record the very brief head movements that primates' make, and in defining these glances have included a time requirement for the behavior. Interestingly, the time requirements for glances in some studies exceed the time requirements for "scans" in others (Table 4). Such inconsistencies in definition have massive implications for the comparability of results across studies.

3.3 | A call for consistency: the behavior of "looking"

Despite there being over 50 published studies of primate vigilance, a general review of methodological approaches has been lacking. Treves' (2000) review stands out as the main attempt to do this thus far, but stops short of exploring methodological differences in great deal and focuses mainly on phenomena related to group size. Nevertheless, it appears that a significant outcome of Treves' work has been the adoption of operational multifunctional definitions. We advocate that this should be standard practice going forward. Attempts to measure "markers" of vigilance have the embedded assumption that an animal needs to be vigilant in order to detect a predator. In contrast it seems reasonable to suggest that an animal looking in the correct direction will have an equal chance of detecting a predator regardless of their intended gaze focus or motivation (Treves, 1998, 1999a, 1999b, 1999c, Treves et al., 2001, 2003). Instead, therefore, we should move away from studying vigilance per se, and instead focus attention on studying the behavior of looking. In this context, we define an individual as looking if:

> *"Its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with".*

This definition is tied to a key prediction however, that any form of looking behavior (in which the focal animal essentially focuses beyond an arm's reach) should reveal a predator or other threat if it is present. In essence it suggests that animals can collect multiple types of information concurrently and that different information acquisition pathways are compatible. If, as seems likely, animals are under consistent pressure to be attentive to numerous different visual stimuli (food, mates, threats, etc.) then pre-emptive vigilance is essentially just one facet of this broader looking activity. Analytically, the behavior can be explored in conjunction with the same sorts of predictor variables used in existing vigilance studies (e.g., number of near neighbors, height above ground, habitat visibility, etc.). In doing so it opens up the potential for hypotheses not related to threat detection to be investigated. Intriguingly, if the behavior of looking beyond an arm's reach will likely detect a predator with reasonable probability regardless of the intended function of looking, it raises the question of whether these animals need to actively search their environment for predators. Will looking for other fitness enhancing tasks (foraging, avoidance of intraspecific competition, mating opportunities) provide adequate predator detection without dedicated "vigilance"?

TABLE 5 Observation methodology in studies of primate vigilance

Sampling methodology	Total number of studies	References
Total number of studies utilizing continuous focal observations	37	See Table 6
Total number of studies utilizing instantaneous sampling (focal interval, scan or point samples)	16	Baldellou & Henzi (1992), Boinski et al. (2003), Caine (1987), Campos & Fedigan (2014), Cowlishaw (1998), de Ruiter (1986), Hardie & Buchanan-Smith (1997), Hill & Cowlishaw (2002), Isbell & Young (1993), Josephs et al. (2016), Kutsukake (2006), McNelis & Boatright-Horowitz (1998), Pannozzo et al. (2007), Robinson (1981), Smith, Kelez & Buchanan-Smith (2004)[a], van Schaik & van Noordwijk (1989)
Total number of studies utilizing one-zero sampling	7	Bshary & Noë (1997), Fragaszy (1990), Gosselin-Ildari & Koenig (2012), Koenig (1998), Steenbeek et al. (1999), Suzuki & Sigiura (2011), Tsingalia & Rowell (1984)

[a] Utilized instantaneous scan sampling and continuous focal sampling.

Determining the answer to this question will require carefully planned studies, but should be a highly profitable avenue for future research. This likely goes beyond what can be done with observational studies, therefore experimental approaches, such as through simulated predator attacks (Kaby & Lind, 2003; Lima & Bednekoff, 1999) will undoubtedly be needed. The key is to design ingenious experiments that constrain individuals to certain behaviors or postures, and test predator detection capabilities. There will be a necessary level of variation across these studies as experiments must focus on the unique attributes of the local predator guilds. This variation shouldn't necessarily be a problem as the outcome should reflect accurate detection probabilities for each study group. Going forward, any study of vigilance behavior (on a given species or group) will benefit from robust and complimentary empirical data defining the informational capacities of the body postures of the relevant study species.

Related to our recommendations, we advise that future work moves away from attempts to tease apart any of the subtypes of looking behavior, such as “anti-predator vigilance” or “social monitoring”, during data collection since an unambiguous assessment of what an animal is looking at is unachievable at all times. Although the outcome from statistical analysis can shed light on which components contribute to individual or group looking behaviors when assessed alongside appropriate socio-ecological variables that effectively capture their animals' perception of fear, attempts to ascribe definitions of subtypes of looking will likely re-establish the inconsistencies highlighted earlier. This is not a call for the cessation of studies of vigilance, however. Rather, it is to advocate for variables associated with anti-predator vigilance to be assessed within the broader looking framework.

4 | VARIATION IN SAMPLING METHODOLOGY

A host of sampling methodologies are available to behavioral ecologists studying animal vigilance; focal animal sampling and scan sampling (or instantaneous scan sampling) seem to be the most popular (Hirschler, Gedert, Majors, Townsend, & Hoogland, 2016), although one-zero sampling has also been utilized in primate vigilance work (Table 5). Typically, continuous focal sampling is advantageous in vigilance studies as it allows observers to record duration measures for vigilance, in addition to frequency measures. However, there is variation in how these measures are manipulated for analysis and subsequently reported. Frequency measures are typically reported as vigilance rates based on the duration of the focal observations (Alberts, 1994; Chapman & Chapman, 1996; Cords, 1990; MacIntosh & Sicotte, 2009; Maestripieri, 1993; Teichroeb & Sicotte, 2012) but the same information can also be reported simply as a frequency measure (Barros, Alencar, Silva, & Tomaz, 2008; Kazahari & Agetsuma, 2010). When individuals are easily identifiable and subject to repeated observations, a number of authors have chosen to average their frequency measure by individual (Cords, 1995; Keverne et al., 1978) although frequency measures have also been averaged per observation session, grouping data from all individuals instead (Nunes, Gonçalves, Emile, & Barros, 2010). Despite utilizing 60-s continuous focal samples to record within-group surveillance in redtail monkeys and red colobus, Treves (1999c) reported the percentage of focal samples containing at least one glance toward another conspecific. Manipulating vigilance into a binary variable was deemed more reliable than utilizing a frequency measure due to the inherent difficulties in recording within-group surveillance reliably.

Studies recording duration measures for vigilance typically average individual vigilance bout durations, either for each experimental trial (Barros et al., 2008) or each focal observation (Hirsch, 2002; Nunes et al., 2010), although bout lengths can be overlooked with total time spent vigilant instead averaged for each individual across all observations (Caine, 1984). Individual vigilance bouts have also been cumulatively summed across a focal observation, allowing a duration measure to be calculated (Gaynor & Cords, 2012; Gould et al., 1997; Kutsukake, 2007; Treves, 1998, 1999a). Another alternative has divided cumulative duration measures by total observation time, producing either vigilance rates (Gould, 1996; Hall & Fedigan, 1997; Treves, 1999c; Watson et al., 2015) or proportion/percentage of time spent vigilant (Busia et al., 2016; Caine & Marra, 1988; Cowlishaw et al., 2004; Jack, 2001; Onishi & Nakamichi, 2011; Rose & Fedigan, 1995; Stojan-Dolar & Heymann, 2010; Treves et al., 2001, 2003), although vigilance rates per

TABLE 6 Continuous focal observation lengths in studies of primate vigilance

Continuous focal observation length	Number of studies	References
10 s	1	Hirsch (2002)
30 s minimum	1	Watson et al. (2015)
30–120 s	2	Onishi & Nakamichi (2011), Stojan-Dolar & Heymann (2010)
60 s	8	Chapman & Chapman (1996), Cords (1990, 1995), Smith, Kelez & Buchanan-Smith (2004)[a], Treves (1998, 1999a,b,c)
90 s	1	Gaynor & Cords (2012)
2 min	4	Treves et al. (2001), Treves et al. (2003), Treves & Brandon (2005), Kutsukake (2007)
3 min	1	Caine & Marra (1988)[b]
5 min	2	Caine (1984), Keverne et al. (1978)[b]
8 min	1	Kazahari & Agetsuma (2010)
10 min	6	Alberts (1994), Gould et al. (1997), Hall & Fedigan (1997), Macintosh & Sicotte (2009), Rose & Fedigan (1995), Teichroeb & Sicotte (2012)
15 min	5	Busia et al. (2016), Dunbar (1983), Gould (1996), Gould et al. (1997)[b], Jack (2001)
20 min	1	Nunes et al. (2010)[b]
30 min	2	Barros et al. (2008)[b], Maestripieri (1993)[b]
Unspecified	3	Cowlishaw et al. (2003), Nowak et al. (2016), Watts (1998)

[a]Utilized instantaneous scan sampling and continuous focal sampling. [b]Captive studies

minute (Nowak, Richards, le Roux, & Hill, 2016) and per hour (Gould et al., 1997) have also been used.

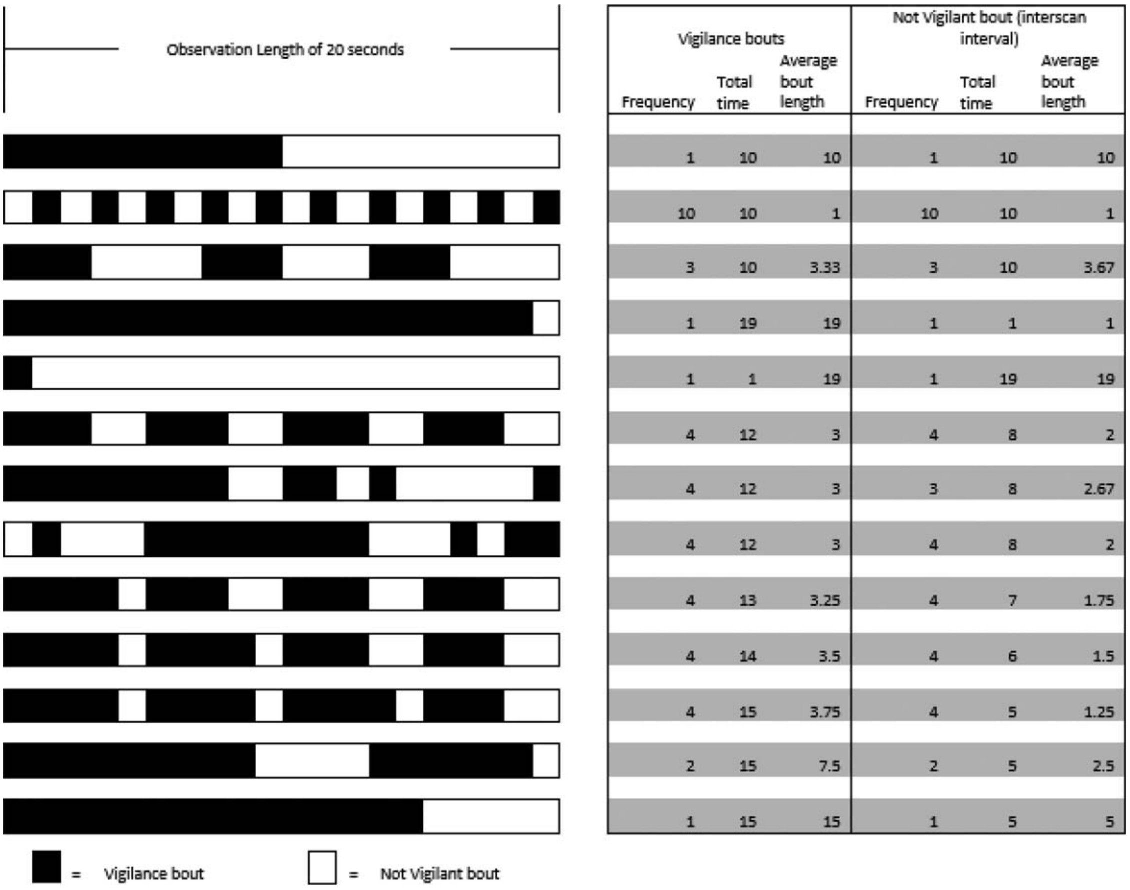
Considerable variability exists in sample durations across studies utilizing continuous focal sampling (Table 6). Captive environments appear to have offered some authors the potential to utilize longer durations for focal sampling (Barros et al., 2008; Maestripieri, 1993; Nunes et al., 2010) than would be practically achievable in the wild, where the majority use samples of 5 min or less, with many using 60 s samples. Short sampling periods are an effective method to minimize the likelihood of aborted samples, require socio-ecological variables to be updated less frequently, and reduce observer fatigue. It is unclear whether the degree of variation found in focal observation lengths could influence the equivalency of results, and a broad comparative assessment of the consistency of results from different methodologies is needed.

Instantaneous scan sampling and focal point/interval sampling (Altmann, 1974) allow authors to calculate the percentage of samples scored as vigilant. There is variability, however, in how these estimates are calculated. Percentages are typically calculated by dividing the number of vigilant “scans” by the total number of “scans” recorded within a group or age-sex class (de Ruiter, 1986; Isbell & Young, 1993; van Schaik & van Noordwijk, 1989). Vigilance has also been reported as a percentage of total scans collected on a given day (Smith et al., 2004), and percentage of total scans collected across an entire study period, for each categorical level of the conditional variables investigated (Robinson, 1981). Alternatively, these percentages can be calculated for each individual study subject over the study period (Josephs et al., 2016; Kutsukake, 2006), or for each individual within each month (Baldellou & Henzi, 1992), or time period (Caine, 1987). Time spent vigilant may also be broken down for a range of behavioral and habitat categories (Cowlishaw, 1998) and Pannozzo et al (2007) calculated the percentage of “social looks” out of the total of “social” and “non-social” looks. Alternatively, model approaches allow researchers to include vigilance state as binary response variable (Campos & Fedigan, 2014).

One-zero sampling has been used sparingly in primate vigilance literature thus far, and its use is rarely advocated in behavioral studies (Altmann, 1974). Where applied, however, the number of intervals containing vigilance can be used directly in subsequent analysis (Bshary & Noe, 1997) but more commonly the frequency of vigilant intervals is expressed as a proportion of total interval frequency, yielding percentage of vigilance. Percentages can be expressed per individual (Tsingalia & Rowell, 1984), experimental condition (Koenig, 1998), age-sex class (Fragaszy, 1990; Gosselin-Ildari & Koenig, 2012), or for each socio-ecological condition under investigation (Gosselin-Ildari & Koenig, 2012; Steenbeek et al., 1999; Suzuki & Sugiura, 2011).

A key factor in one-zero sampling is the choice of interval length, which has proved variable in primate vigilance literature, varying from 5 s (Gosselin-Ildari & Koenig, 2012; Koenig, 1998) though 10 s (Bshary & Noe, 1997), 30 s (Tsingalia & Rowell, 1984) and 60 s (Steenbeek et al., 1999; Suzuki & Sugiura, 2011) intervals. In addition, Fragaszy (1990) used one-zero sampling to record the predominant activity occurring in the first 5 s of consecutive 15-s intervals. Such variability undoubtedly undermines the comparability of results.

All the methods discussed earlier should in theory produce similar if not identical results, and indeed a number of authors have made this assumption (Hill & Cowlishaw, 2002; Smith et al., 2004). Thus far,



Vigilance bouts			Not Vigilant bout (interscan interval)		
Frequency	Total time	Average bout length	Frequency	Total time	Average bout length
1	10	10	1	10	10
10	10	1	10	10	1
3	10	3.33	3	10	3.67
1	19	19	1	1	1
1	1	19	1	19	19
4	12	3	4	8	2
4	12	3	3	8	2.67
4	12	3	4	8	2
4	13	3.25	4	7	1.75
4	14	3.5	4	6	1.5
4	15	3.75	4	5	1.25
2	15	7.5	2	5	2.5
1	15	15	1	5	5

FIGURE 1 Example vigilance schedules and the information that can be extracted from each strategy, adapted from Beauchamp (2015)

however, there has been little research to test this assertion. Hirschler et al. (2016) recently compared results from two different sampling methods used to record vigilance patterns in Gunnison's prairie dogs (*Cynomys gunnisoni*): continuous focal sampling and instantaneous scan sampling. Vigilance estimates produced from scan sampling were found to be consistently and significantly higher than the estimates produced from continuous focal sampling. It also highlighted that the use of alert/non-alert criteria in their vigilance definitions made instantaneous assessments of vigilance more challenging than focal sampling the duration of vigilance. In primates, Rose (2000) compared continuous and point samples within a focal sampling protocol for white-faced capuchins and found that, overall, the two focal sampling methods produced similar activity budgets for most behaviors. However, time spent eating was noticeably higher in datasets collected using a continuous protocol, whilst interval sampling seemed to produce lower estimates for time allocated to foraging and movement behaviors. Most importantly, vigilance estimates were slightly lower for interval sampling versus continuous sampling. These results were attributed to omission of rare behaviors in interval sampling (i.e., behaviors of short duration such as glances), and conditional sampling biases in continuous sampling (i.e., under-representing certain behaviors such as fast movement).

The tendency for authors to analyze average vigilance-bout lengths or convert vigilance information into percentage or proportion measures also highlights another area of interest. Thus far, the temporal organization of vigilance (Beauchamp, 2015), or vigilance scheduling (McVean & Haddlesey, 1980) has received little attention, particularly in primates. Vigilance scheduling refers to the different strategies an animal can use to achieve vigilance. For example, an animal can achieve 10 s of vigilance in a set length of time through a single 10-s bout, or through 10, brief, 1-s glances. In both cases 10 s of vigilance is achieved, but through very different strategies. Equally, the organization of inter-scan interval (periods of non-vigilance) can vary, and should not be overlooked (Figure 1). A key point here is how to approach the coding of datasets, as both recording the frequency of bouts and averaging vigilance information across an observation period clearly removes a lot of important information (Figure 1). This issue has essentially been overlooked in primate vigilance studies, with numerous different approaches found. With a switch in focus to studying looking, we believe there is a now an opportunity to develop a consistent approach to tackling this problem going forward, as there is clearly room for a great degree of behavioral flexibility in looking scheduling.

4.1 | A call for consistency: Sampling methodology

In addition to researchers adopting a common definition, a convergence of sampling methodologies is also required. Although different methodologies should in theory give similar results for specific questions, many preclude the ability to look at vigilance scheduling and the temporal organization of vigilance (Beauchamp, 2015). It is thus recommended that studies move towards the use of continuous focal sampling, and where possible, video-recording focal observations. Although, this may be challenging for certain populations, short focal observation lengths (such as <1 min) should be viable across a wide range of contexts. The advantage of video footage is that researchers can extract precise information on the duration of looking bouts, and can additionally extract a host of alternative measures such as frequency of looking, or interval between looking bouts. Multiple measures increase the scope of the questions that can be addressed.

Importantly, such an approach would start to address the fact that numerous studies have included arbitrary time requirements in their vigilance definitions (Table 4). It is recommended that researchers report "looking distributions" in future work to enable readers to understand how study groups utilize different lengths of looking bouts. These distributions could be used to identify clusters of bout durations that might represent a functional difference in use. For example, consistent bout durations between say 0.3 and 0.9 s could represent animals using quick bouts, or "glances", to rapidly update information on the environment. In contrast, extensive looking bouts of 30 s or more might be consistent with a classification of scanning. The key point here is that researchers move away from arbitrary definitions of different aspects of vigilance prior to data collection and instead use their quantified looking distributions to understand whether subcategories might exist and whether there are significant patterns in the temporal scheduling of looking. At the same time these looking distributions will be informative in selecting an ideal focal observation length. If the individual bout durations utilized by a study group consistently exceed the length of the focal observation, then bout durations will be artificially truncated (Treves et al., 2001), leading to biased and unreliable results. For example, if members of a study group consistently utilize looking bouts exceeding 30 s in duration, then 30-s focal observation lengths would be inappropriate. Where possible, future work should attempt to use similar focal observation lengths, particularly where working on the same species or at the same study site, although this should never come at the cost of biasing results via systematic sampling errors.

5 | FUTURE OPPORTUNITIES IN THE BEHAVIOR OF LOOKING

Despite a wealth of factors receiving thorough investigation in studies of primate vigilance thus far, our review found some key areas have received less attention, or have been overlooked entirely. These represent interesting opportunities for future work in the framework of looking. Although Alberts (1994) reported that the glance rates of juvenile female baboons decreased between 6 and 24 months of age, ontogeny effects otherwise appear to have been largely overlooked. Favreau et al. (2014) explored the possibility that individual variation in vigilance use by eastern gray kangaroos (*Macropus giganteus*) and its trade-off with feeding rates could be governed by age-related factors, such as diminishing body and bite size with age. These factors could lead to older individuals occupying a phenotype that is at greater risk of predation, which could then directly influence the vigilance patterns exhibited by these individuals. Ontogeny effects could drive differences in visual capabilities, with juveniles experiencing underdeveloped systems and lacking knowledge to utilize gaze attention effectively, and older individuals suffering from diminished visual acuity (Davidson & Clayton, 2016; Fernández-Juricic, Erichsen, & Kacelnik, 2004). Some age-related effects have been reported in primate vigilance studies, with juveniles of both sexes typically less vigilant than adults (Boinski et al., 2003; de Ruiter, 1986; Fragaszy, 1990; Gosselin-Ildari & Koenig, 2012), although Watson et al. (2015) reported the opposite effect. This was the only paper to investigate the heritability of vigilance, however, in this case estimated at 12% for rhesus macaques (Watson et al., 2015). Primate groups often contain numerous non-adult individuals that are consistently excluded from sampling efforts. If these individuals are able to contribute to predator detection then they could be a vital component in collective detection. It is strongly encouraged that future work investigates all individuals within their study groups to understand the impact that different age-sex classes have on threat detection.

Anthropogenic factors have also been largely overlooked in primate vigilance work thus far. Nowak et al. (2016) found that cage-trapping and subsequent re-exposure to cage-trap stimulus had no effect on vigilance rates in samango monkeys (*Cercopithecus albogularis schwarzi*). However, factors such as habitat modification or anthropogenic noise pollution have not received investigation. Treves and Brandon (2005) found no evidence for tourism influencing the vigilance use of black howler monkeys but showed that monkeys increased their distances to observers during intense interactions with tourists and increased their height from the ground in response to the size of tourist parties, suggesting tourist presence is far from neutral for these monkeys. Equally, it is unclear whether factors such as habituation level or the human shield-effect (Berger, 2007; Nowak, Le Roux, Richards Scheijen, & Hill, 2014) are consistent across individuals within groups, or across different groups and species.

In captivity, experimental apparatus could exclude observer effects on vigilance (Barros et al., 2008; Caine, 1984; Nunes et al., 2010), but these are more challenging to control in wild environments. Looks towards observers have been recorded and excluded (Koenig, 1998; Pannozzo et al., 2007), simply not recorded (Suzuki & Sugiura, 2011), or grouped with other forms of reactionary vigilance and classified as "anti-predator" vigilance (Hirsch, 2002). MacIntosh & Sicotte (2009) recorded and retained vigilance data in which study animals directed vigilance towards observers and other humans, leading to human related factors being considered as possible driver of vigilance use in ursine colobus. Despite these studies representing good attempts to account for vigilance directed at observers, they overlook the idea that the presence of an observer or multiple observers could alter an animal's perception of fear, for both predation and social threats, and therefore influence its vigilance patterns as a result. Treves and Brandon (2005) reported that increasing number of observers led to increased distances between monkeys and observers; even though a vigilance response was not detected the behavioral adjustments made by the monkeys suggest observer related effects are worthy of greater attention. Treves et al. (2001) likely accounted for some of these elements by including number of observers as a control factor in their analysis.

Altough technology isn't fully available to allow observers to capture the looking behaviors exhibited by wild primate groups in the absence of observers (but see Nowak et al., 2016), we should not overlook the fact that the presence of observers could also be a key determinant of "looking". Just as the influence of an animal's height from the ground or number of neighbors on "looking" patterns could be subject to variation across different individuals, so too can the degree to which individuals tolerate the presence of observers. The scale of response by individual study subjects to observers could arguably range from a flee-on-sight response; to a tendency for certain individuals to "observe" observers, in each case these fundamental personality traits could be a key determinant of individual "looking" behaviors. Future work that explores ways to capture this information and include it within multivariate analysis would be valuable.

Any group-level patterns or trends must be driven by individual group members adapting to different conditions. For example, individual nutmeg mannikins (*Lonchura punctulata*) experimentally placed into groups of different sizes showed that some individuals were consistently more vigilant than others, regardless of group size (Rieucau, Morand-Ferron, & Giraldeau, 2010). Similarly, high inter-individual differences in vigilance use have been reported in eastern gray kangaroos (Edwards, Best, Blomberg, & Goldizen, 2013), to the extent some individual kangaroos can cancel out a group-size effect on vigilance by devoting more effort to social vigilance (Carter, Pays, & Goldizen, 2009). Such issues undoubtedly extend to primates. Inter-individual differences have often been overlooked, or treated as background noise, and numerous multivariate approaches now include individual as a random effect. However, this practice will overlook some of the precise drivers underlying individual vigilance patterns. An interesting avenue would be to explore individual vigilance profiles (Beauchamp, 2015), and furthermore utilize these profiles to define strategies that can be factored into future simulation models exploring the behavior of looking and threat detection. Many primates are excellent study species for these questions.

6 | CONCLUSIONS

Studies of vigilance have had a long history in primatology, with research exploring a wide range of potential drivers of vigilance in a diversity of socio-ecological conditions. An emerging feature of this work has been the variability of the relationships reported; something that appears, in part, to relate to fundamental differences in the methods employed across studies and inconsistencies in definitions of vigilance behavior. Greater consistency is therefore needed. In his recent review of animal vigilance Beauchamp (2015) identified a series of unanswered questions: Is vigilance for predators compatible with looking for scrounging opportunities? Are vigilant animals better able to detect a predator sooner? Has the incompatibility between vigilance and other activities been exaggerated? How do animals coordinate their vigilance in groups and does it conform to the assumption of randomness of vigilance that underpins theoretical models? What about nocturnal species? Or animals on islands and so subject to reduced predator pressure? What about humans as predators? Primates should be a good study system for many of these issues. With a consistent approach to defining looking, and a robust methodology that permits the multifaceted dimensions of looking to be addressed, future studies of primate vigilance are likely to be a profitable avenue of enquiry that has the potential to place primatology at the forefront of animal vigilance research.

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REFERENCES

Alberts, S. C. (1994). Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. *Animal Behaviour*, *47*, 749–755.

Altmann, J. (1974). Observational study of behavior: Sampling. *Behaviour*, *49*, 227–267.

Baldellou, M., & Henzi, P. S. (1992). Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Animal Behaviour*, *43*, 451–461.

Barros, M., Alencar, C., Silva, M. A D S., & Tomaz, C. (2008). Changes in experimental conditions alter anti-predator vigilance and sequence predictability in captive marmosets. *Behavioural Processes*, *77*, 351–356.

Bates, H. W. (1863). *The naturalist on the river amazon*. London: Murray Press.

Beauchamp, G. (2015). *Animal vigilance: Monitoring predators and competitors*. London: Academic Press.

Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology and Evolution*, *13*, 284–287.

Belt, T. W. (1874). *The naturalist in Nicaragua*. London: Murray Press.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*, 620–623.

Blanchard, P., & Fritz, H. (2007). Induced or routine vigilance while foraging. *Oikos*, *116*, 1603–1608.

Boinski, S. U. E., Kauffman, L., Westoll, A., Stickler, C. M., Cropp, S., & Ehmke, E. (2003). Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (Saimiri oerstedii, S. boliviensis, S. sciureus). *Behaviour*, *139*, 1421–1467.

Bshary, R., & Noe, R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, *54*, 1461–1474.

Burger, J., & Gochfeld, M. (1988). Effects of group size and sex on vigilance in ostriches (Stuthio camelus): Antipredator strategy or mate competition? *Ostrich: Journal of African Ornithology*, *59*, 14–20.

Busia, L., Schaffner, C. M., & Aureli, F. (2016). Watch out or relax: Conspecifics affect vigilance in wild spider monkeys (Ateles geoffroyi). *Behaviour*, *153*, 107–124.

Caine, N. G. (1984). Visual scanning by tamarins. *Folia Primatologica*, *43*, 59–67.

Caine, N. G. (1987). Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (Saguinus labiatus). *American Journal of Primatology*, *12*, 241–250.

Caine, N. G., & Marra, S. L. (1988). Vigilance and social organization in two species of primates. *Animal Behaviour*, *36*, 897–904.

Cameron, E. S. (1908). Observations on the golden eagle in Montana. *The Auk*, *XXV*, 251–268.

Campos, F. A., & Fedigan, L. M. (2014). Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology*, *25*, 477–486.

Carter, A. J., Pays, O., & Goldizen, A. W. (2009). Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. *Behavioral Ecology and Sociobiology*, *64*, 237–245.

Chance, M. R. A. (1967). Attention structure as the basis of primate rank orders. *Man*, *2*, 503–518.

Chapman, C. A., & Chapman, L. J. (1996). Mixed-species primate groups in the kibale forest: Ecological constraints on association. *International Journal of Primatology*, *17*, 31–50.

Cords, M. (1990). Vigilance and mixed-species associations of some East African forest monkeys. *Behavioral Ecology and Sociobiology*, *26*, 297–300.

Cords, M. (1995). Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, *132*, 559–569.

Cowlishaw, G. (1998). The role of vigilance in the survival and reproductive strategies of Desert Baboons. *Behaviour*, *135*, 431–452.

Cowlishaw, G., Lawes, M. J., Lightbody, M., Martin, A., Pettifor, R., & Rowcliffe, J. M. (2004). A simple rule for the costs of vigilance: Empirical evidence from a social forager. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 27–33.

Davidson, G. L., & Clayton, N. S. (2016). New perspectives in gaze sensitivity research. *Learning & Behavior*, *44*, 9–17.

Davis, D. E. (1941). The Belligerency of the Kingbird. *The Wilson Bulletin*, *53*, 157–168.

de Ruiter, J. R. (1986). The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (Cebus olivaceus). *Behaviour*, *98*, 240–258.

Dehm, M. M. (1990). Vigilance for predators: Detection and dilution effects. *Behavioral Ecology and Sociobiology*, *26*, 337–342.

Dimond, S., & Lazarus, J. (1974). The problem of vigilance in animal life. *Brain, Behavior and Evolution*, *9*, 60–79.

Dunbar, R. I. M. (1983). Structure of gelada baboon reproductive units: IV. Integration at group level. *Zeitschrift Für Tierpsychologie*, *63*, 265–282.

Edwards, A. M., Best, E. C., Blomberg, S. P., & Goldizen, A. W. (2013). Individual traits influence vigilance in wild female eastern grey kangaroos. *Australian Journal of Zoology*, *61*, 332–341.

Elgar, M. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, *64*, 13–33.

Favreau, F. R., Goldizen, A. W., Fritz, H., Blomberg, S. P., Best, E. C., & Pays, O. (2014). Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos. *Animal Behaviour*, *92*, 175–184.

Fernández-Juricic, E., Erichsen, J. T., & Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends in Ecology and Evolution*, *19*, 25–31.

Fragaszy, D. (1990). Sex and age differences in the organisation of behaviour in wedge-capped capuchins, Cebus olivaceus. *Behavioral Ecology*, *1*, 81–94.

Galton, F. (1871). Gregariousness in cattle and in men. *Macmillan's Magazine*, *23*, 353–57.

Gaynor, K. M., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour*, *84*, 531–537.

Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*. Chichester: Princeton University Press.

Gosselin-Ildari, A. D., & Koenig, A. (2012). The Effects of Group Size and Reproductive Status on Vigilance in Captive Callithrix jacchus. *American Journal of Primatology*, *74*, 613–621.

Gould, L. (1996). Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (Lemur catta) at the Beza-Mahafaly Reserve, Madagascar. *International Journal of Primatology*, *17*, 331–347.

Gould, L., Fedigan, L. M., & Rose, L. M. (1997). Why Be Vigilant? The Case of the Alpha Animal. *International Journal of Primatology*, *18*, 401–414.

Hall, K. R. L. (1960). Social vigilance behaviour of the chacma baboon, Papio ursinus. *Behaviour*, *16*, 261–293.

Hall, K. R. L. (1962). Numerical data, maintenance activities and locomotion of the wild chacma baboon, Papio ursinus. *Proceedings of the Zoological Society of London*, *139*, 181–220.

Hall, C. L., & Fedigan, L. M. (1997). Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, *53*, 1069–1082.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295–311.

Hardie, S. M., & Buchanan-Smith, H. M. (1997). Vigilance in single- and mixed-species groups of tamarins (Saguinus labiatus and Saguinus fuscicollis). *International Journal of Primatology*, *18*, 217–234.

Hartley, P. H. T. (1947). Review: Predation by sparrow-hawk populations. *Ecology*, *28*, 326–328.

Haude, R. H., Graber, J. G., & Farres, A. G. (1976). Visual observing by rhesus monkeys: Some relationships with social dominance rank. *Animal Learning & Behavior*, *4*, 163–166.

Hausfater, G., & Takacs, D. (1987). Structure and Function of Hindquarter Presentations in Yellow Baboons (Papio cynocephalus). *Ethology*, *74*, 297–319.

Hill, R. A. & Cowlishaw, G. C. (2002) *Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations*. In: L. E Miller (Ed.) Eat or be eaten: predator sensitive foraging among primates (pp. 187–204). Cambridge: Cambridge University Press.

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, *52*, 458–464.

Hirschler, I. M., Gedert, J. L., Majors, J., Townsend, T., & Hoogland, J. L. (2016). What is the best way to estimate vigilance? A comparison of two methods for Gunnison's prairie dogs, Cynomys gunnisoni. *Animal Behaviour*, *121*, 117–122.

Holder, C. F. (1885). *Marvels of animal life* (1st ed.). New York: Scribner's sons.

Isbell, L. A., & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behavioral Ecology and Sociobiology*, *32*, 377–385.

Jack, K. M. (2001). Effect of Male Emigration on the Vigilance Behavior of Coresident Males in White-faced Capuchins (Cebus capucinus). *International Journal of Primatology*, *22*, 715–732.

Jenkins, D. W. (1944). Territory as a result of despotism and social organization in geese. *The Auk*, *61*, 30–47.

Josephs, N., Bonnell, T., Dostie, M., Barrett, L., & Peter Henzi, S. (2016). Working the crowd: Sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology*, *27*, 988–994.

Kaby, U., & Lind, J. (2003). What limits predator detection in blue tits (Parus caeruleus): Posture, task or orientation? *Behavioral Ecology and Sociobiology*, *54*, 534–538.

Kazahari, N., & Agetsuma, N. (2010). Mechanisms determining relationships between feeding group size and foraging success in food patch use by Japanese macaques (Macaca fuscata). *Behaviour*, *147*, 1481–1500.

Keverne, E. B., Leonard, R. A., Scruton, D. M., & Young, S. K. (1978). Visual monitoring in social groups of talapoin monkeys (Miopithecus talapoin). *Animal Behaviour*, *26*, 933–944.

Koenig, A. (1998). Visual scanning by common marmosets (Callithrix jacchus): Functional aspects and the special role of adult males. *Primates*, *39*, 85–90.

Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology*, *112*, 581–591.

Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. *International Journal of Primatology*, *28*, 907–918.

Leopold, F. (1951). A study of nesting wood ducks in Iowa. *The Condor*, *53*, 209–220.

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: The group-size effect. *Animal Behaviour*, *49*, 11–20.

Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack?. *Animal Behaviour*, *58*, 537–543.

MacIntosh, A. J. J., & Sicotte, P. (2009). Vigilance in ursine black and white colobus monkeys (Colobus vellerosus): An examination of the effects of conspecific threat and predation. *American Journal of Primatology*, *71*, 919–927.

Maestripieri, D. (1993). Vigilance costs of allogrooming in macaque mothers. *American Society of Naturalists*, *141*, 744–753.

Marler, P. (1956). Behaviour of the chaffinch Fringilla coelebs. *Behaviour. Supplement*, *5*, 1–184.

McNamara, J. M., & Houston, A. I. (1992). Evolutionarily stable levels of vigilance as a function of group size. *Animal Behaviour*, *43*, 641–658.

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Animal Cognition*, *1*, 65–69.

McVean, A., & Haddlesey, P. (1980). Vigilance schedules among House Sparrows Passer domesticus. *Ibis*, *122*, 533–536.

Miller, R. C. (1922). The significance of the gregarious habit. *Ecology*, *3*, 122–126.

Mueller, T., Fagan, W. F., & Grimm, V. (2011). Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, *4*, 341–355.

Nowak, K., Le Roux, A., Richards, S. A., Scheijen, C. P. J., & Hill, R. A. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology*, *25*, 1199–1204.

Nowak, K., Richards, S. A., Le Roux, A., & Hill, R. A. (2016). Influence of live-capture on risk perceptions of habituated samango monkeys. *Journal of Mammalogy*, *97*, 1461–1468.

Nunes, D. M., Gonçalves, I., Emile, N., & Barros, M. (2010). Bimodal temporal organization of specific vigilance behaviors in captive black tufted-ear marmosets (Callithrix penicillata). *Behavioural Processes*, *84*, 629–631.

Onishi, K., & Nakamichi, M. (2011). Maternal Infant Monitoring in a Free-ranging Group of Japanese Macaques (Macaca fuscata). *International Journal of Primatology*, *32*, 209–222.

Oswald, F. L. (1885). The animal soul. *The North American Review*, *141*, 122–136.

Oxford Dictionary. (2017). Vigilance - definition of vigilance in English | Oxford Dictionaries. Retrieved August 1, 2017, from https://en.oxforddictionaries.com/definition/vigilance

Pannozzo, P. L., Phillips, K. A., Haas, M. E., & Mintz, E. M. (2007). Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (Cebus apella). *Ethology*, *113*, 881–888.

Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. *Animal Behaviour*, *22*, 501–505.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, *38*, 419–422.

Rieucau, G., Morand-Ferron, J., & Giraldeau, L. A. (2010). Group size effect in nutmeg mannikin: Between-individuals behavioral differences but same plasticity. *Behavioral Ecology*, *21*, 684–689.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, *51*, 1077–1086.

Robinson, J. G. (1981). Spatial structure in foraging groups of wedge-capped capuchin monkeys Cebus nigrivittatus. *Animal Behaviour*, *29*, 1036–1056.

Rose, L. M. (2000). Behavioral sampling in the field: Continuous focal versus focal interval sampling. *Behaviour*, *137*, 153–180.

Rose, L. M., & Fedigan, L. M. (1995). Vigilance in white-faced capuchins, Cebus capuchinus, in Costa Rica. *Animal Behaviour*, *49*, 63–70.

Smith, A. C., Kelez, S., & Buchanan-Smith, H. M. (2004). Factors affecting vigilance within wild mixed-species troops of saddleback (Saguinus fuscicollis) and moustached tamarins (S. mystax). *Behavioral Ecology and Sociobiology*, *56*, 18–25.

Steenbeek, R., Piek, R. C., van Buul, M., & van Hooff, J. A. R. A. M. (1999). Vigilance in wild Thomas's langurs (Presbytis thomasi): The importance of infanticide risk. *Behavioral Ecology and Sociobiology*, *45*, 137–150.

Stojan-Dolar, M., & Heymann, E. W. (2010). Vigilance in a cooperatively breeding primate. *International Journal of Primatology*, *31*, 95–116.

Suzuki, M., & Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. *American Journal of Primatology*, *73*, 623–631.

Teichroeb, J. A., & Sicotte, P. (2012). Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (Colobus vellerosus). *Behavioral Ecology and Sociobiology*, *66*, 453–466.

Treves, A. (1998). The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour*, *135*, 453–481.

Treves, A. (1999a). Has predation shaped the social systems of arboreal primates? *International Journal of Primatology*, *20*, 35–67.

Treves, A. (1999b). Vigilance and Spatial Cohesion among Blue Monkeys. *Folia Primatologica*, *70*, 291–294.

Treves, A. (1999c). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology*, *48*, 113–126.

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*, 711–722.

Treves, A., & Brandon, K. (2005). *Tourist impact on the behavior of black howler monkeys (Alouatta pigra) at Lamanai, Belize*. In J. D. Paterson & J. Wallis (Eds.), Commensalism and conflict: The human-primate interface (pp. 147–167). Norman, OK: American Society of Primatologists.

Treves, A., Drescher, A., & Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (Alouatta pigra). *Behavioral Ecology and Sociobiology*, *50*, 90–95.

Treves, A., Drescher, A., & Snowdon, C. T. (2003). Maternal watchfulness in black howler monkeys (Alouatta pigra). *Ethology*, *109*, 135–146.

Tsingalia, H. M., & Rowell, T. E. (1984). The behaviour of adult blue monkeys. *Zeitschrift Für Teirpsychologie*, *64*, 253–268.

van Schaik, C., & van Noordwijk, M. (1989). The special role of male Cebus monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology*, *24*, 265–276.

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, *30*, 405–422.

Watson, K. K., Li, D., Brent, L. J. N., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A. V., . . . Platt, M. L. (2015). Genetic influences on social attention in free-ranging rhesus macaques. *Animal Behaviour*, *103*, 267–275.

Watts, D. P. (1998). A preliminary study of selective visual attention in female mountain gorillas (Gorilla gorilla beringei). *Primates*, *39*, 71–78.

Williams, J. J. (1903). On the use of sentinels by valley quail. *The Condor*, *5*, 146–148.

SUPPORTING INFORMATION

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Chapter 3. Implications of varied definitional ethoses

Definition and interpretation effects: How different vigilance definitions can produce varied results

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AA conceived and coordinated the study, collected all field data, carried out statistical analysis, and drafted the initial manuscript. AA and RH designed the study with equal contribution. RH participated in statistical analysis and critically revised the manuscript.

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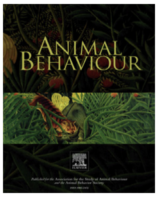

Commentary

Definition and interpretation effects: how different vigilance definitions can produce varied results

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Animals use vigilance to detect or monitor threats. While numerous aspects of vigilance have been studied across a wide range of species, little work has explored the methodological variation that has emerged across these studies. Different approaches in sampling designs, statistical analyses and definitions can make cross-study comparisons challenging and potentially obscure our understanding of animal vigilance. In this study we explore two important components of vigilance definitions and ask (1) whether definitions vary in their interobserver agreement, and (2) whether using different definitions can create varied results within and across observers. Separate groups of 'experienced' and 'inexperienced' observers extracted data from video focal observations of wild chacma baboons, *Papio ursinus*, using four different definitions representative of the variation found within primate vigilance literature. In the first stage of analysis, we found that the four definitions varied in their interobserver agreement, with only an operational-looking definition performing well across both duration and frequency assessments, and an experienced/inexperienced dichotomy. This suggests definitions vary in how well observers can converge on similar interpretations of the same definition. The second part of the analysis used the experienced group's data in a typical primate vigilance analysis and found results varied within observers across definitions, i.e. definition effects, and across observers within definitions, i.e. interpretation effects. Together these results suggest that variation in definitions and their interpretation could have a fundamental role in producing between-study differences in results. Future vigilance research must consider these factors and explore working towards a single framework for studying vigilance, particularly within taxonomic families. Without consistency, cross-study comparisons are likely to be challenging and future observational work on other behaviours may also benefit from exploring these types of definitional issues. For baboons, operationalized definitions appear the most consistent across observers; however, future research should explore its application in other taxa.

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Understanding how animals use vigilance to detect and avoid predators (among other threats) has proved a popular topic for animal behaviour research, with bird species generally receiving the most attention (Beauchamp, 2015). Birds have offered researchers an excellent study system, as their postural changes are relatively straightforward to monitor (Beauchamp, 2017), with 'head raising' or 'head up' postures used as markers for vigilance (Beauchamp, 2018; Fernandez et al., 2003; Klett-mingo et al., 2016). Such definitions have been common in vigilance research, seemingly since the model of Pulliam (1973), which inferred 'head cocks' allowed birds to detect predators. As vigilance research has grown, however, variation in vigilance definitions has become expansive, with a variety of definitions emerging (Allan & Hill, 2018; Beauchamp, 2015).

Potentially because of the predominant focus on vigilance patterns in birds, numerous mammalian vigilance studies have followed a similar postural paradigm in defining vigilance. For example, in a general review of mammalian vigilance patterns, Quenette (1990) defined vigilance as 'a head lift interrupting the ongoing activity, and followed by a visual scanning of the environment'. Comparable definitions have been used in studies on antelopes (Lian et al., 2007), sheep (Brown et al., 2010; Rieucau & Martin, 2008), kangaroos (Carter et al., 2009; Favreau et al., 2010), capybara (Yaber & Herrera, 1994), marmots (Ferrari et al., 2009; Shriner, 1998), squirrels (Arenz & Leger, 2000; Shriner, 1998), primates (Alberts, 1994), lizards (Ito & Mori, 2010; Javier &

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Perez-Mellado, 2000) and fish (Brandl & Bellwood, 2015). Nevertheless, as the taxonomic focus of vigilance work has broadened, variation in vigilance definitions has emerged. In most part this is due to different species having different postural capabilities and tendencies but can also be attributed to the specific focus of individual studies. Many studies on mammalian species have taken into account the distinction between quadrupedal and bipedal (Bednekoff & Blumstein, 2009; Blumstein et al., 2010; Quirici et al., 2008; Vasquez, 1997) or 'vertical' postures (Unck et al., 2009). Vigilance research on birds has also applied additional constraints to vigilance, such as the requirement of 'side to side movement of the head' (Elgar & Catterall, 1981), 'stood still, with necks fully extended' (Burger & Gochfeld, 1988), or 'extending ('stretching') the head upwards and looking around while standing straight' (Li et al., 2017). Similarly, in lizards, definitions have been based on a range of factors, including 'head movement' when stationary (Ito & Mori, 2010), 'eyes open' (Lanham & Bull, 2004) and 'pause' in locomotor activity (Lopez & Martin, 2013), while Iberian wall lizards, *Podarcis hispanica*, were considered vigilant when immobile/paused and had their 'head high, their eyes raised', and 'rarely moving their heads side to side' (Javier & Perez-Mellado, 2000).

Subtler variation can also be found across studies on similar species. For example the following definitions have been used for *Cebus* monkeys: 'animal had its head-up and looked around, providing it was not inspecting vegetation or partners at close range' (van Shaik & van Noordwijk, 1989), 'scanning intently at long range while alert and stationary' (Campos & Fedigan, 2014), 'cautiously observing the surroundings, often with horizontal rotation of the head' (de Ruiter, 1986) and 'visual inspection of surrounding area without a fixed gaze; turning head side to side' (Fragaszy, 1990). Across a number of different geese species vigilance has typically been defined using 'head up' or 'extreme head up' postures (Forslund, 1993; Kahlert, 2003; Shimada & Shimada, 2003); however, other examples include 'head was above the level of its back' (Atkins et al., 2019) and 'head held in an upright position, looking around and alert' (Tadeo & Gammell, 2018). The nuanced variation that has emerged in vigilance definitions may be required to sample the unique postural and behavioural traits of each species and may be ecologically valid and necessary from a methodological perspective. However, some variation appears to have emerged not out of necessity but through vigilance research lacking a consolidated framework. Little is known, however, about whether variation at the definition level could alter the distribution of data sets collected, and thus results, making comparisons of findings across different individuals, groups and species challenging.

In addition, little work has explored the repeatability of individual definitions, i.e. how well different researchers or observers converge on similar interpretations of the same definitions. As the list of more technical definitions has expanded it is unclear whether certain requirements are challenging for observers to reach agreement on and so lead to inconsistencies between independent studies. Some definitions contain elements that ask observers to interpret aspects of the animal's behaviours and state which could be prone to varied interpretations, for example scanning intently (Campos & Fedigan, 2014), visual scanning of the environment (Quenette, 1990), looking around and alert (Tadeo & Gammell, 2018); however, postural definitions such as head up or head raising could also vary in interobserver agreement, for example do all researchers agree on the exact point the animal's head is up? Is this consistent across different studies and species?

In this study we use the variation in definitional ethos found throughout primate vigilance research as a framework to investigate these questions. Primates use a range of postures and have the ability to handle food items while looking around concurrently (Cowlishaw et al., 2004). Potentially as a result of these factors, primate vigilance studies have used a plethora of definitions despite primates being relatively understudied compared to other taxa in terms of vigilance (Beauchamp, 2015). This has potentially generated the highest degree of variability in vigilance definitions for a single taxon within the literature (see Allan & Hill, 2018). Nevertheless, there seems to be a clear dichotomy between studies interested in reactionary and those investigating pre-emptive aspects of vigilance. Studies focusing on reactionary vigilance appear to use postural changes associated with danger recognition such as 'active visual search skyward with an exacerbated posture' (Boinski et al., 2003). In contrast, studies of pre-emptive vigilance focus on data collected in the absence of threatening events (Teichroeb, 2017). This is complicated in primates, however, as numerous species also need to monitor both within- and extragroup conspecific threats (see Allan & Hill, 2018). Pre-emptive vigilance markers are likely to be much more subtle (reducing the cost to the animal) and therefore challenging to identify (Allan & Hill, 2018). As most primate vigilance research has focused on the pre-emptive form of vigilance, we concentrate exclusively on it here.

In this study we identify four distinct definitional ethoses within primate vigilance literature. First, a number of definitions are descriptive in nature, using visual terminology to describe the behavioural markers of interest, for example 'cautiously observing' (de Ruiter, 1986), 'gazing into the distance', 'gazing/gazes fixed on the surrounding environment' (Kutsukake, 2006, 2007), 'visual inspection of surrounding area' (Fragaszy, 1990). Second, a number of studies have used and adapted the postural framework (e.g. head movement) found commonly in bird literature (see Allan & Hill, 201). Examples include 'movement of the head and/or eyes' (Gaynor & Cords, 2012), 'continuous head movement of at least 45 degrees in any direction' (MacIntosh & Sicotte, 2009) and 'sweeping/single movement of the head' (Barros et al., 2008; Nunes et al., 2010). A third type of definition uses a nonoperationalized scanning/looking approach, recording a basic posture and inferring nothing about the animal's line of vision, for example 'eyes were open and its head up' (Cowlishaw, 1998; Hill & Cowlishaw, 2002).

Finally, operationalized scanning/looking definitions have also been used. For example, Treves' (e.g. Treves, 1998) scanning definitions 'scanning/visual search directed beyond arm's reach' or Allan & Hill's (2018) looking definition 'Its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with' ask observers to interpret when the animal is looking beyond its immediate vicinity, assuming this increases the animal's chances of detecting a predator regardless of what it is actually looking for or at. This definitional ethos is not focused on sampling vigilance specifically (see Treves, 1998 and Allan & Hill, 2018 for discussion); instead, the aim is to sample whenever an animal's field of vision is such that it could detect a predator if it was there, regardless of its precise focus of attention. As such, much more general looking/scanning behaviours are recorded under the premise that scanning/looking and threat detection share complete compatibility. Studies adopting the definition of Treves (1998) have still frequently reported evidence regarding numerous vigilance hypotheses, highlighting that vigilance can still be detected analytically despite making no attempt to specifically sample a state of vigilance (see Allan & Hill, 2018).

We used a group of habituated Afromontane chacma baboons, *Papio ursinus griseipes*, as a model system to explore how the variation in vigilance definitions found in primate vigilance studies may impact on data consistency and repeatability. We constructed four representative definitions based on the definitional ethoses above to test the hypothesis that different definitions may contain inherent variability relating to their interobserver reliability. This also allowed us to assess whether differences in vigilance definition can then lead to varied results. The definitions were: (1) visual terminology: ‘animal is gazing at or visually inspecting its surroundings’; (2) head/eye movement: ‘animal's head is up combined with side-to-side movement of the head and/or eyes'; (3) non-operationalized looking/scanning: ‘its head is up and eyes open’; (4) operationalized looking/scanning: ‘its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with’.

Predictions are challenging. Concise definitions (e.g. head up, eyes open) or definitions using verbs to describe behavioural/biological markers (e.g. gazing or inspection) could generate a greater degree of interobserver variance. Alternatively, more complex operationalized definitions could result in observers struggling to converge on identical interpretations. Regardless, we investigate the reliability of the definitions themselves via interobserver/rater agreement tests. An important issue when using experienced researchers to collect behavioural data is that they may have previously used a specific protocol, or several protocols, in the past. As such, each individual observer may be influenced by their initial and ongoing training interacting with their own experiences. We explore this notion in this study by using two separate groups of ‘experienced’ and ‘inexperienced’ observers.

Each definition and the unique interpretation of each definition by each observer may also produce differences in the distribution of data sets generated, and we assessed the magnitude of this variation and investigated whether it could influence the outcome of the results following a typical mixed-model vigilance analysis. We explored whether a number of widely investigated contextual factors (see Allan & Hill, 2018) could influence looking/vigilance patterns differently depending on the definition used. We included number of neighbours within 5 m, distance to nearest neighbour, habitat type (open/closed) and spatial position (central or peripheral) as these can also tie into hypotheses related to within-group and external threats (Allan & Hill, 2018). To incorporate the foraging—vigilance trade-off, we also included the time the animal spent performing ‘engaged’ behaviours, i.e. foraging and grooming.

This analysis is not focused on observer effects per se (i.e. the differences between observers within a study, or the impact of an observer on an animal's behaviour) but instead focuses on definition effects (i.e. differences in results due to the use of different definitions) and interpretation effects (i.e. differences in results between studies due to different interpretations of the same definition). Definition effects are unlikely to occur within a single study as researchers should not adopt multiple definitions of the same behaviour. Instead, definition effects are most likely to occur between different studies. If definition effects are apparent in this study, then we would expect varying results within observers and across definitions. Interpretation effects can overlap with observer effects within studies (e.g. several observers collecting vigilance data at the same time), but the focus of this study is to mimic occasions where multiple independent studies adopt similar definitions, and to explore whether the results are comparable in these instances. If interpretation effects are apparent in this study, then we would expect varying results within definitions and across observers.

METHODS

Study Area

This research was undertaken under ZA/LP/81996 research permit, with ethical approval from the Animal Welfare Ethical Review Board (AWERB) at Durham University. We collected our data on a wild habituated group of chacma baboons at Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo, South Africa (23°02′S, 29°26′E). The study area included a complex mosaic of habitats within a variable mountainous environment (Willems & Hill, 2009) and all the natural habitats belonged to the Afromontane mist-belt communities and varied in their structural characteristics, including canopy height, foliage density and refuge availability (Coleman & Hill, 2014). Most of the land within the study area was classified as a private nature reserve; however, agricultural practices take place locally and overlap with the core part of the study group's home range (Williams et al., 2017). Known predators of the baboons in the study area include leopards, *Panthera pardus*, and rock python, *Python sebae*, while the study group has also been observed to act fearfully and alarm-call at a number of raptor species and brown hyaenas, *Hyaena brunnea*.

Study Group

Owing to long-term anthropogenic activities in the study area (local farming and residences), consistent interactions with humans have been ongoing with this population for some time. The study group was formerly habituated ca. 2005 and received periods of research attention up until 2014. Since 2014 the study group received consistent observational research in the form of full day follows (generally 3—4 days a week), with occasional gaps of up to 5 weeks. The group was typically followed dawn to dusk on a schedule of 4 days on and 3 days off designed to maintain as much of their natural interactions with predators as possible. The study group contained between 85 and 90 individuals over the course of the study (June 2018 to December 2018); several disappearances occurred during this period but their causes were unconfirmed. A.A. had followed and collected behavioural and spatial data on this group since early 2015 and was able to identify all individuals including juveniles and infants based on their unique physical characteristics.

Video Sampling Methodology

All focal samples were completed solely by A.A. using a high-definition video camera (Panasonic HC-W580 Camcorder) to record all focal observations. Continuous focal sampling is the only method to capture detailed information on the temporal organization of vigilance/looking (Allan & Hill, 2018; Beauchamp, 2015; McVean & Haddlesey, 1980) and so we focused only on comparisons using a continuous focal sampling framework. Following a pilot study exploring the ideal focal observation length for this study group, we used 30 s continuous focal animal sampling to collect vigilance/looking data across the full range of behaviours and habitat types. These short duration focal samples were appropriate for sampling the study animals' visual behaviours since the average bout length was often less than 1 s and the duration of the focal observation was rarely the same duration as time spent looking/vigilant. Across experienced observers, definition 1 produced 11.8% of samples with the duration of ‘vigilance’ equal to the observation length, while 2.2% of samples contained 0 s of vigilance, and 14% of samples had an average bout length of less than 1 s. The respective information for the remaining definitions was as follows: definition 2: 8%, 17.8% and 4.2%; definition 3: 11.8%, 2.6% and 15.2%; and definition 4: 12.4%, 0% and 13.8%.

Short sampling periods are also an effective method to minimize the likelihood of aborted samples, require contextual variables to be updated less frequently and reduce observer fatigue. When contextual factors are updated frequently it becomes challenging to manipulate and code data in a way that effectively explains the scenarios underpinning the focal observation; as such, short focal observations are an ideal solution to identify the precise drivers influencing the focal animal's current behaviour. Owing to the difficulties associated with continuous focal sampling of moving animals a number of studies have excluded travelling activities (Gaynor & Cords, 2012; Smith et al., 2004; Stojan-Dolar & Heymann, 2010; Treves, 1998, 1999; Treves et al., 2001, 2003). As there is no prior expectation that baboons cannot detect threats if moving or do not collect visual information during travelling behaviours, it could form an important component of their looking repertoire, and thus was retained.

To control for time of day, we split the day into four time periods that were adjusted seasonally to ensure each accounted for 25% of the current daylength. We produced a randomly ordered list of all individuals in the group (excluding neonates and dependent infants) and selected focal individuals pseudorandomly. The first individual encountered from the top 15 names (ca. 20% of original group-size) on the list was sampled immediately by A.A. If greater than 50% of the focal animal's face was out of sight for more than 5 s, the focal observation was aborted. A.A. would then adjust his position and attempt to restart the focal observation after a 1 min break. This process was attempted a maximum of three times, after which A.A. would move on to sampling another individual from the list. The aborted focal individual was then reintegrated at the end of the list.

Prior Training of ‘Experienced’ and ‘Inexperienced’ Observers

Using the focal video observations collected solely by A.A., we asked an additional nine observers (plus A.A.) to code these observations according to each definition. Four experienced observers (excluding A.A.) were all previously trained to collect ‘scanning’ data on habituated samango monkeys, *Cercopithecus albogularis schwarzi*, in field conditions using the definition ‘scanning directed beyond arm's reach’ (see Treves, 1998). Each of these observers received identical training and testing and had completed at least 2 months of behavioural data collection in the field prior to this study. This was the first primate behaviour and vigilance sampling experience each observer had received, so background knowledge should have been similar. The experience of sampling using the definition of Treves (1998) may have interacted with the interpretation (of each definition) by this pool of observers and is very similar to the operationalized looking definition (definition 4) used in this study. To explore this, we enlisted a further five ‘inexperienced’ observers (no previous experience studying vigilance in any organism or of collecting behavioural data on primates).

Extracting Vigilance Information from Video Footage

We restricted the analysis to data collected on 18 individual adult females to limit the number of variables influencing the results; sex differences in vigilance and ontological effects have been reported in primates (see Allan & Hill, 2018). Looking/vigilance data were extracted from focal videos independently by the 10 different observers (including A.A.) using the video playback software Media Player Classic (MPC-HC: Guliverkli project). Videos could be slowed down to extract precise looking bout lengths (video skip length could be reduced to four hundredths of a second when played back at quarter speed). The start and end time for each looking/vigilance bout was ascertained from the media player and entered into an Excel spreadsheet, allowing two dependent variables to be calculated post hoc for analysis: duration of time spent looking/vigilant and frequency of looking/vigilance bouts. Each focal video observation could be viewed as many times as needed, allowing precise information to be recorded. If the focal animal was deemed to be vigilant/looking at the onset of the focal observation, then bouts were considered to start with the commencement of the observation period. Similarly, an ongoing bout would be deemed to end at the end of the focal observation. If an observer felt that less than 50% of the focal animal's face was out of sight, this was coded as time spent out of sight and offset in model analyses (see below).

Video-coding Procedure for Observers

Each observer coded a number of focal sample videos using the different vigilance definitions. To make comparisons as robust as possible, all data were extracted from the same set of videos. The experienced group (plus A.A.) coded 10 focal videos for 18 individual female baboons (180 focal videos in total) for each definition. For the inexperienced group, we used eight videos from a smaller subset of eight individuals taken from the same data set (64 videos coded in total) for each definition; these had also been coded by the experienced observers, allowing for comparisons. To act as a baseline for comparison, the inexperienced group were first asked to sample when they felt the animal was ‘vigilant’. No further description was provided, or discussion of what vigilance may or may not mean. As such, we could assess the agreement for ‘vigilance’ within this group independent of definitions given subsequently.

The study was split into four distinct phases. Within each phase an observer was asked to extract data for a specific definition. To minimize biases, each observer ran through the entire set of videos once for a single definition, before beginning to extract data for a different definition. Each observer was given a single definition at a time and asked to make their own interpretation of the definition before beginning the coding process and did not receive the next definition until coding the previous definition was complete. Observers were each given the definitions in a different order to mitigate against order effects, although the focal videos themselves were generally done in the same order (although an observer could choose to go through videos multiple times, so there may have been some sequencing discrepancy within definitions as a result). They could not return to another definition once it was completed.

Study authors did not guide observers towards specific interpretations. Our reason for doing this was to mimic how researchers may adopt the vigilance definitions of other researchers when replicating a study, thus providing insight into whether interpretation effects could exist between independent studies. Some guidance was necessary, however, to ensure each observer created precise interpretations (i.e. based on their favoured behavioural, postural or visual markers) that were consistently implemented across all observations. A.A. therefore encouraged all observers to think about the true meaning of each term or phrase (e.g. gazing, inspection, side to side, line of vision, etc.), while additionally offering a range of postural (e.g. angle or height of the head from the ground), behavioural (e.g. raising or turning of the head) and visual cues (e.g. eye movement, direction of vision) for them to consider in their interpretations. All suggested cues were clearly observable as opposed to factors linked with the internal state of an animal, such as scanning intently, cautiously observing or watchfulness, which have been used in primate vigilance research (see Allan & Hill, 2018). A.A. used the same standard advice for all observers and kept a record of the cues each observer used, and the challenges they communicated while implementing each definition.

Each observer extracted data four times from each focal video, once for each definition given previously. The inexperienced group also extracted data for the fifth definition, ‘vigilance’, prior to the other four definitions. All observers agreed not to discuss their observations during each coding phase or for the duration of the study and they were not able to code videos concurrently when in the same room. A.A. coded videos separately from the others and was the only participant not blind to the study design.

Contextual Variables

While videoing focal observations in the field, A.A. recorded several contextual factors at the beginning and end of the 30 s focal observation. We used number of neighbouring conspecifics within 5 m, distance to nearest neighbour, habitat type (open/closed) and spatial position (central or peripheral) as contextual variables that may predict vigilance use in baboons (Allan & Hill, 2018). The number of (all noninfant) neighbours or distance to nearest neighbour values were averaged for each focal observation between the start value (at 0 s) and end value (at 30 s/end of focal observation). A.A. had validated their ability to assess both distance measures during pilot work but a calibrated laser range finder (Leica DISTO DXT) was used to assess distance to the nearest neighbour if there were ever any accuracy concerns.

Habitat type and spatial position were assessed at the end of the focal observation. Habitat type was considered open when the focal animal was in areas without canopy cover (e.g. grassland, rock, cliff, marshland, road, camps, farm) and closed when canopy was present (e.g. bushland, woodland, forest). Spatial position of the focal animal was determined via assessment of visual and audible cues given by other group members. An individual was considered peripheral if on the edge of the group or had no more than five noninfant individuals between itself and the edge of the group. We used the focal videos to record the duration of engaged (foraging, grooming, self-grooming, handling food items) and not engaged (resting, moving, receiving grooming, chewing food items) behaviours during a focal observation; and included this as another covariate predictor of vigilance use.

Calculating Interobserver Reliability Using Concordance Correlation Coefficient

Assessing interrater reliability has traditionally used Pearson correlation coefficients, paired *t* tests or Bland–Altman plots, but the intraclass correlation coefficient (ICC) has become more popular recently, especially when assessing reliability on continuous variables using multiple observers (Hernaez, 2015; Koo & Li, 2016). As most of our data sets did not meet the assumptions of ICC analysis, we instead calculated concordance correlation coefficients (CCC), estimated using a variance components analysis (see Carrasco et al., 2013). This method is recommended in this scenario as it does not require the ANOVA assumptions of ICC analysis (Chen & Barnhart, 2013) and has been shown to be identical to ICC when observers were treated as a fixed effect and agreement between ratings was being investigated (Carrasco & Jover, 2003).

The data extraction protocol allowed for duration and frequency of bouts to be calculated for each focal observation. The CCC analysis was undertaken for both measures separately using a range of different groupings of observers. We first grouped all experienced observers together, with and without data produced by A.A. As A.A. had completed several years of observational data collection on three monkey species and sampled several different vigilance or scanning definitions through this time, he had a different background to the other experienced observers and was also aware of the purpose of the investigation. We grouped the inexperienced observers together (separately from experienced observers) as they were the only group to assess ‘vigilance’ and their CCC estimates were not as influenced by their training background and prior experiences. Finally, we grouped all observers' data together, with and without A.A. As inexperienced observers coded a subset of data from the larger data set, these CCC estimates were based only on focal observations that both sets of observers had coded, i.e. the 64 videos coded by the inexperienced observers. Grouping all observers together allowed insights into whether the experienced and inexperienced groups produced consistent data to one another, as opposed to exploring the consistency within each observer grouping.

We calculated CCC using the ‘cccvc’ function from the ‘cccrm’ package (version 1.2.1; Carrasco & Martinez, 2015), using the software R (version 3.5.0, R Core Team, 2019). Since the focus of the study was to understand reliability within definition types, we did not require observers to code dummy data sets prior to this study and achieve an a priori level of interrater reliability before starting this study (Hallgren, 2012); the training aspect was simply to inform each observer of the extraction methodology and detail how data should be entered. All observers made assessments for every focal video on every individual baboon, making this study a fully crossed design (Hallgren, 2012).

The variance components model used for CCC estimation calculates the mean deviation of each observer from the overall mean across subjects and observers (Carrasco et al., 2013); in ICC terms this equates to the mean being used as the assessment basis for CCC estimation (Koo & Li, 2016). In ICC analyses a definition must be selected depending on whether absolute ‘agreement’ or ‘consistency’ is to be investigated. We designed this study to explore agreement between observers only, that is, we were interested in whether multiple observers can produce similar values, as opposed to ‘consistency’ which tests whether observers' ratings tend to produce similar rank orders (Hallgren, 2012; Koo & Li, 2016).

Focal observations with fewer bouts or less time devoted to vigilance or looking activities clearly have less potential for discrepancy between observers than focal observations where vigilance/looking is frequent. In addition, when values for either dependent variable was lower, small discrepancies between observers could lead to higher variability between them relative to discrepancies between observations with higher observed levels of vigilance/looking. However, these factors are not issues within this analysis as all observers coded the same set of video observations (i.e. fully crossed design) across a diverse range of looking/vigilance values. As such, to get excellent agreement (i.e. CCC > 0.9) almost identical assessments are required across observers (within observations) for a high proportion of observations.

Mixed-Model Analysis Assessing Consistency of Trends Across Definitions and Observers

The data produced for each definition by each ‘experienced’ observer plus A.A. were used for this aspect of the analysis. Duration and frequency measures (produced from each definition, by each observer) were used as separate response variables in several generalized linear mixed-effects models; each observer had four models with duration as a response variable and four models with frequency as the response variable, each based on the data for the four definitions coded. Each model was fitted using a Bayesian procedure and the same contextual variable predictors. The time the focal animal had at least 50% of its face in view (never less than 25 s) was included as an offset variable in all models, for example if the animal's face was out of view for 2 s then the observation length was updated to 28 s within the offset variable. Individual baboon ID was fitted as a random factor. In all cases the error distribution for the duration (s) response models was Gaussian and Poisson for the frequency (count) response models, each with default link functions. Default Student t priors ($df = 3$, mean $= 0$, Scaling Factor $= 10$) were assigned to all model components.

All models were fitted using the brm function from the brms package (Bürkner, 2017) in the R software (R Core Team, 2019). The brm function commands samples to be drawn from the posterior distribution via the package Rstan (Stan Development Team, 2019), which interfaces with the probabilistic programming language Stan

(The Stan C++ Library, version 2.17.3) via the C++ toolchain in Rtools (R Core Team, 2018). The brm function implements Hamiltonian Monte Carlo (Duane et al., 1987; Neal, 2003) in combination with the No-U-Turn Sampler (NUTS) extension (Hoffman & Gelman, 2014), resulting in algorithms that converge efficiently, even for complex models (Hoffman & Gelman, 2014). For each model we ran six Hamiltonian Markov chains for 10 000 iterations to provide algorithms that converge efficiently for multilevel models (Bürkner, 2017); these were both set higher than default settings to aid fitting a relatively small sample size. In addition, we set warmup to 4000 (higher than default). This sets the number of warmup iterations used for stepwise adaptation and allows the sampling algorithm to hone in on efficient values for step size and the number of steps used for sampling (Bürkner, 2017; McElreath, 2019). Warmup iterations were discarded and not used for sampling; using a higher warmup than default improves sampling efficiency and aids in modelling of the entire posterior distribution including potentially extreme tails (McElreath, 2019).

To aid with issues relating to a small sample size Adapt_delta was set to 0.99; this reduces the step size (which controls the resolution of the NUTS sampler) forcing the NUTS sampler to slow down, producing more robust posterior samples. Across all models there was no evidence of divergent transitions. The Gelman–Rubin convergence diagnostic (Rhat, Gelman & Rubin, 1992) was used to assess Markov Chain Monte Carlo convergences by comparing the estimated within- and between-chain variances of each factor within the model. Rhat was equal to 1 in all cases, indicating accuracy of the response variables with regard to the Gaussian/Poisson response distributions, i.e. the standard deviation of duration/frequency points formed around the corresponding Guassian/Poisson functions was minimal. In all models, the bulk and tail estimated sample size was greater than 10 000 for all fixed effects.

Although we principally examined the estimates, 95% credible intervals and conditional effects from each model, this process can be subjective and lead to incorrect interpretations of results (Kruschke, 2018). Therefore, we additionally calculated the 89% highest density interval (HDI) of the posterior distribution of each model. The HDI reveals the upper and lower parameter values of the posterior distribution based on all points within the 89% interval, points within the interval therefore have a higher probability density than points outside the interval (Kruschke & Liddell, 2018). Although any arbitrary percentage value could be implemented for the HDI, 89% has been recommended due to it providing improved stability over using 95% (McElreath, 2019). We also calculated the probability of direction (pd) for each fixed effect for each model. The pd variable is an index for inspecting effect existence and highlights the certainty that a particular effect has directionality (i.e. is positive or negative); pd ranges from 50% (i.e. equal distribution of positive and negative posterior values) to 100% (e.g. all posterior values are either positive or negative). In addition, pd has been shown to have a 1:1 correspondence with *P* values derived using frequentist methods (Makowski et al., 2019).

To reduce potential for inconsistent interpretations of results we developed an a priori set of rules for deducing results. We used two criteria for accepting the null hypothesis: (1) when the HDI overlapped or included zero and (2) when the pd was less than 90%. This would mean at least a proportion of the most credible parameter values include zero while pd indicates little certainty in the effect having directionality. In all other circumstances the null was rejected, and we classified results as ‘effect has some uncertainty’, ‘moderate evidence for an effect’ and ‘strong evidence for an effect’. In all of these scenarios there needed to be some evidence for a relationship between a covariate and the dependent variable, i.e. a positive/negative estimate, evidence of a consistent relationship in conditional effects plots. Moderate evidence for an effect required that the HDI did not overlap or include zero and that the pd was at least 90%, the only difference to strong evidence was that the pd was higher than 97.5%. There were numerous cases of detecting positive/negative estimates with noticeable trends between the covariate predictors and the dependent variable, and the pd was at least 90 or 95%, but the HDI marginally overlapped or included zero. These cases still suggest some evidence of an effect, but there was uncertainty, and these results were coded accordingly. All estimates and HDI values displayed in the tables in the Results were coded according to the HDI–pd decision rules to aid visual interpretation.

RESULTS

Interobserver Reliability

The experienced group produced excellent agreement for duration of vigilance/looking for two of four definitions (see Table 1, definitions 1 and 4), with definition 3 approaching excellent agreement. The effect was reduced for frequency estimates, with only definition 4 approaching excellent agreement. The operationalized definition 4 seems to be the most repeatable for both duration and frequency, although the visual terminology definition 1 is close among experienced observers, particularly for duration assessments. The inexperienced group produced almost identical agreement results (compared to experienced) for duration and frequency for definition 4; this held when their data were combined with those of experienced observers, including and not including A.A. For inexperienced observers, agreement was moderate for duration of definition 1; estimates were considered poor for 2 and 3, although definition 3 was moderate for combined assessments. Agreement was moderate (for duration) among inexperienced observers for the ‘vigilance’ definition, which was greater than the agreement they produced for definitions 2 and 3. Agreement was poor (for frequency) among inexperienced observers for four of five definitions but was again slightly higher for ‘vigilance’ than for definitions 1, 2 and 3.

Consistency of Trends Across Definitions and Observers

The mixed-model analysis assessing the consistency of trends with contextual variables for the duration measure found examples of results remaining consistent in direction and magnitude within observers across definitions (see Table 2). However, there were also several examples of results differing. For example, observer 1's data found evidence of an effect for time spent engaged in definitions 1 and 4, but this effect had uncertainty in definition 3, while the H0 was accepted in definition 2. Generally, each definition produced similar directionality of results for the duration response variable, although a small number of cases reported an opposing trend. Model estimates and HDI parameter values were generally consistent across observers for definitions 1 and 3, although both have examples of varied results. Definition 4 was also consistent and found similar estimates and HDI parameter values across all variables; however, the uncertainty around some results could lead to varied interpretations. Definition 2 produced the most varied results with the spatial position variable producing both strong and moderate evidence for three observers but accepting the H0 in the remaining two.

Agreement of results was lower for the frequency measure compared to the duration measure (Table 3), with variable results within observers across definitions and within definitions across observers. The model estimates and HDI parameter values were fairly consistent for the engaged variable; however, some minor differences were apparent. The number of neighbours within 5 m

Table 1
Concordance correlation coefficient (CCC) estimates for duration and frequency measures, across experienced and inexperienced observers and definitions 1–5

	(1) Visual terminology	(2) Head/eye movement	(3) Nonoperationalized	(4) Operationalized	(5) 'Vigilance'
	CCC (95% CI)	CCC (95% CI)	CCC (95% CI)	CCC (95% CI)	CCC (95% CI)
Duration					
Experienced	0.939 (0.924,0.951)[a]	0.602 (0.538,0.659)[c]	0.899 (0.875,0.918)[b]	0.973 (0.966,0.978)[a]	
Experienced (excluding A.A.)	0.949 (0.936,0.960)[a]	0.538 (0.466,0.602)[c]	0.899 (0.874,0.919)[b]	0.967 (0.958,0.974)[a]	
Inexperienced	0.570 (0.454,0.666)[c]	0.241 (0.151,0.328)	0.452 (0.345,0.547)	0.943 (0.918,0.961)[a]	0.508 (0.392,0.609)[c]
Combined	0.740 (0.658,0.804)[c]	0.403 (0.305,0.493)	0.662 (0.571,0.737)[c]	0.965 (0.951,0.976)[a]	
Combined (excluding A.A.)	0.722 (0.636,0.790)[c]	0.366 (0.269,0.455)	0.634 (0.539,0.713)[c]	0.962 (0.946,0.974)[a]	
Frequency					
Experienced	0.763 (0.715,0.804)[b]	0.309 (0.242,0.374)	0.683 (0.625,0.734)[c]	0.880 (0.852,0.903)[b]	
Experienced (excluding A.A.)	0.767 (0.718,0.809)[b]	0.234 (0.165,0.302)	0.74 (0.686,0.786)[c]	0.882 (0.853,0.906)[b]	
Inexperienced	0.233 (0.130,0.331)	0.004 (−0.045,0.05)	0.204 (0.110,0.294)	0.848 (0.787,0.892)[b]	0.243 (0.137,0.343)
Combined	0.458 (0.354,0.552)	0.098 (0.05,0.15)	0.352 (0.249,0.447)	0.868 (0.818,0.905)[b]	
Combined (excluding A.A.)	0.432 (0.326,0.527)	0.06 (0.017,0.103)	0.330 (0.231,0.422)	0.863 (0.811,0.901)[b]	

CI: credible interval.

[a] Excellent correlation estimates (>0.9).

[b] Good correlation estimates (>0.75 and <0.9).

[c] Moderate correlation estimates (>0.5 and <0.75); no asterisk represents poor correlation estimates (<0.5).

variable produced consistent directionality; however, there was some variation in estimates and HDI parameter values across definitions and observers. Despite this, definitions 1 and 4 produced the most consistent results. It could be argued that the average nearest-neighbour distance generally produced posterior values relatively close to zero and as such there is little evidence supporting an effect in any model. However, several models display a pd greater than 97.5%, indicating strong evidence supporting a negative effect of average nearest-neighbour distance; as such, results clearly varied across definitions and observers. The habitat (open/closed) variable consistently produced posterior estimates that supported the null for definitions 1, 2 and 3; however, for definition 4 three observers' models found moderate or strong evidence supporting a negative effect. Spatial position (central/peripheral) was also relatively consistent in directionality with the H0 accepted for most models, although there was some evidence supporting an effect in the results produced from A.A.'s models for definitions 1 and 2.

For frequency assessments there appears to be strong within-definition agreement between some observers but not others. Examples include A.A., observer 1 and observer 3 producing almost identical posterior estimates and HDI parameter values for definition 4 while observers 2 and 4 produced less substantial evidence. Observers 2 and 3 produced similar estimates and HDI parameter values for definitions 1 and 2 but varied for definitions 3 and 4, while A.A. and observer 1 were consistent for definitions 3 and 4,

Table 2
Summary of model results for duration response variable

	A.A.	Observer 1	Observer 2	Observer 3	Observer 4
(1) Visual terminology: ‘Animal is gazing or visually inspecting its surroundings’					
Intercept	−14.26 (−18.17, −10.44)	−13.31 (−17.07, −9.24)	−11.84 (−15.61, −8.05)	−12.7 (−16.6, −8.82)	−12.21 (−16.08, −8.12)
Engaged	0.09 (−0.02, 0.21)	**0.12 (0.01, 0.25)**[b]	0.1 (−0.01, 0.21)[a]	**0.13 (0.01, 0.25)**[b]	0.11 (−0.01, 0.23)[a]
No. of neighbours	−0.14 (−1.1, 0.79)	−0.08 (−1.02, 0.89)	−0.32 (−1.22, 0.61)	−0.01 (−0.99, 0.92)	−0.21 (−1.17, 0.76)
Neighbour distance	−0.33 (−0.86, 0.18)	−0.25 (−0.77, 0.28)	−0.47 (−0.99, 0.02)[a]	−0.33 (−0.85, 0.2)	−0.25 (−0.78, 0.28)
Habitat	0.2 (−2.37, 2.86)	1.13 (−1.59, 3.7)	−0.05 (−2.58, 2.51)	0.49 (−2.17, 3.19)	0.61 (−2.09, 3.26)
Spatial position	**−2.76 (−5.45, −0.04)**[b]	**−2.99 (−5.72, −0.25)**[b]	−2.46 (−4.99, 0.25)[a]	**−3.18 (−5.8, −0.36)**[b]	**−2.9 (−5.56, −0.09)**[b]
(2) Head/eye movement: ‘Animal's head is up combined with side-to-side movement of the head and/or eyes’					
Intercept	−15.9 (−19.71, −12.23)	−20.22 (−23.62, −16.83)	−9.47 (−12.71, −6.05)	−14.48 (−18.43, −10.52)	−16.15 (−19.8, −12.18)
Engaged	**0.13 (0.02, 0.25)**[b]	0.08 (−0.02, 0.18)	0.02 (−0.08, 0.12)	0.11 (0, 0.23)[a]	0.11 (0, 0.23)[a]
No. of neighbours	−0.16 (−1.06, 0.74)	−0.61 (−1.45, 0.2)	−0.64 (−1.44, 0.18)[a]	−0.08 (−1.03, 0.89)	−0.07 (−0.95, 0.88)
Neighbour distance	−0.33 (−0.82, 0.18)	−0.25 (−0.72, 0.19)	−0.37 (−0.82, 0.07)[a]	−0.26 (−0.77, 0.29)	−0.15 (−0.66, 0.35)
Habitat	0.12 (−2.32, 2.69)	1.02 (−1.28, 3.36)	−0.37 (−2.72, 1.82)	0.34 (−2.32, 3.08)	1.62 (−0.88, 4.22)
Spatial position	**−2.82 (−5.42, −0.24)**[b]	−1.68 (−4.07, 0.65)	−1.13 (−3.48, 1.13)	**−2.97 (−5.8, −0.33)**[b]	**−3.71 (−6.33, −1.02)**[c]
(3) Nonoperationalized looking/scanning: ‘Its head is up and eyes open’					
Intercept	−14.42 (−18.29, −10.48)	−15.26 (−19.07, −11.2)	−15.01 (−18.77, −11.25)	−12.98 (−16.92, −9.1)	−12.15 (−16.22, −8.34)
Engaged	0.09 (−0.03, 0.2)	0.1 (−0.02, 0.22)[a]	0.1 (−0.01, 0.21)[a]	0.12 (0, 0.23)[a]	**0.11 (0, 0.23)**[a]
No. of neighbours	−0.14 (−1.1, 0.79)	0.06 (−0.9, 1.01)	0.05 (−0.87, 0.96)	−0.2 (−1.14, 0.76)	0.1 (−0.83, 1.08)
Neighbour distance	−0.22 (−0.74, 0.3)	−0.37 (−0.91, 0.14)	−0.31 (−0.79, 0.21)	−0.34 (−0.88, 0.17)	−0.23 (−0.74, 0.3)
Habitat	0.94 (−1.76, 3.63)	0.86 (−1.74, 3.6)	0.78 (−1.81, 3.31)	1.47 (−1.18, 4.17)	0.54 (−2.24, 3.12)
Spatial position	**−3.29 (−6.05, −0.55)**[b]	−2.45 (−5.24, 0.25)[a]	−2.59 (−5.29, −0.01)[b]	**−2.84 (−5.49, −0.02)**[b]	**−3.35 (−6.12, −0.62)[b]**
(4) Operationalized looking/scanning: ‘Its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with’					
Intercept	−12.68 (−16.76, −8.94)	−12.59 (−16.4, −8.61)	−13.32 (−17.03, −9.5)	−13.21 (−17.1, −9.44)	−10.45 (−14.24, −6.44)
Engaged	**0.14 (0.03, 0.26)**[b]	**0.13 (0.01, 0.25)**[b]	0.1 (−0.01, 0.22)[a]	**0.12 (0.01, 0.24)**[b]	**0.12 (0, 0.23)**[a]
No. of neighbours	−0.09 (−1.04, 0.86)	−0.14 (−1.09, 0.81)	−0.03 (−0.93, 0.9)	−0.13 (−1.07, 0.8)	−0.29 (−1.23, 0.67)
Neighbour distance	−0.29 (−0.81, 0.23)	−0.3 (−0.83, 0.21)	−0.31 (−0.82, 0.2)	−0.27 (−0.8, 0.23)	−0.36 (−0.86, 0.18)
Habitat	0.64 (−1.95, 3.38)	0.53 (−2.16, 3.14)	0.69 (−1.92, 3.28)	0.6 (−1.98, 3.27)	0.05 (−2.49, 2.74)
Spatial position	**−3.05 (−5.68, −0.21)**[b]	−2.62 (−5.4, 0.05)[a]	**−3.01 (−5.62, −0.35)**[b]	**−2.77 (−5.51, −0.15)**[b]	−2.34 (−5.01, 0.4)[a]

Each column (i.e. A.A., Observer 1. etc) represents each experienced observer; each row represents the fixed effects investigated within each observer's model. Cells are coded with asterisks according to the HDI–pd (highest density interval–probability of direction) decision rule.

[a] An effect has some uncertainty.

[b] Moderate evidence for an effect.

[c] Strong evidence for an effect. Bold cells highlight where the pd was greater than 95%.

Table 3
Summary of model results for frequency response variable

	A.A.	Observer 1	Observer 2	Observer 3	Observer 4
(1) Visual terminology: 'Animal is gazing or visually inspecting its surroundings'					
Intercept	−28.64 (−28.9, −28.39)	−29.08 (−29.34, −28.83)	−28.74 (−28.96, −28.52)	−28.96 (−29.22, −28.72)	−28.76 (−29.03, −28.49)
Engaged	0 (−0.01, 0)	0 (0, 0.01)	0 (−0.01, 0.01)	0 (−0.01, 0.01)	−0.01 (−0.01, 0)[a]
No. of neighbours	**−0.1 (−0.16, −0.04)**[c]	**−0.07 (−0.13, −0.01)**[c]	**−0.06 (−0.11, 0)**[a]	−0.05 (−0.11, 0.01)[a]	−0.04 (−0.1, 0.01)[a]
Neighbour distance	**−0.03 (−0.07, −0.01)**[b]	−0.01 (−0.04, 0.02)	−0.01 (−0.04, 0.01)	−0.02 (−0.05, 0.01)	0 (−0.03, 0.03)
Habitat	−0.1 (−0.24, 0.07)	0.01 (−0.15, 0.17)	0.1 (−0.04, 0.24)	−0.07 (−0.23, 0.09)	−0.03 (−0.18, 0.12)
Spatial position	−0.14 (−0.27, 0.08)[a]	0.05 (−0.12, 0.22)	−0.07 (−0.22, 0.07)	−0.01 (−0.17, 0.16)	0 (−0.15, 0.16)
(2) Head/eye movement: 'Animal's head is up combined with side-to-side movement of the head and/or eyes'					
Intercept	−28.52 (−28.79, −28.23)	−30.14 (−30.59, −29.69)	−29.23 (−29.48, −29.98)	−29.45 (−29.72, −29.16)	−29 (−29.3, −28.71)
Engaged	0 (−0.01, 0.01)	**0.02 (0, 0.03)**[a]	0 (−0.01, 0.01)	0 (−0.01, 0.01)	0 (−0.01, 0.01)
No. of neighbours	**−0.13 (−0.2, −0.06)**[c]	−0.11 (−0.23, 0.01)[a]	−0.03 (−0.1, 0.03)	−0.01 (−0.08, 0.06)	−0.05 (−0.12, 0.02)
Neighbour distance	**−0.09 (−0.12, −0.05)**[c]	−0.05 (−0.1, 0.02)	0 (−0.03, 0.03)	0.01 (−0.03, 0.04)	**−0.05 (−0.09, −0.01)**[c]
Habitat	−0.12 (−0.29, 0.06)	0.01 (−0.28, 0.3)	−0.07 (−0.25, 0.1)	−0.04 (−0.23, 0.15)	−0.02 (−0.21, 0.16)
Spatial position	**−0.23 (−0.41, −0.03)**[b]	−0.08 (−0.38, 0.22)	−0.01 (−0.19, 0.17)	−0.07 (−0.26, 0.13)	−0.06 (−0.24, 0.14)
(3) Nonoperationalized looking/scanning: 'Its head is up and eyes open'					
Intercept	−28.57 (−28.84, −28.3)	−28.79 (−29.04, −28.51)	−29.05 (−29.29, −28.82)	−28.84 (−29.09, −28.59)	−28.98 (−29.24, −28.74)
Engaged	0 (−0.01, 0)	0 (−0.01, 0)	0 (−0.01, 0)	−0.01 (−0.01, 0)[a]	−0.01 (−0.01, 0)[a]
No. of neighbours	**−0.1 (−0.16, −0.04)**[c]	**−0.11 (−0.17, −0.04)**[c]	−0.04 (−0.1, 0.02)	**−0.07 (−0.13, 0)**[a]	−0.04 (−0.1, 0.02)
Neighbour distance	**−0.04 (−0.07, −0.01)**[c]	**−0.05 (−0.08, −0.01)**[c]	−0.01 (−0.04, 0.03)	**−0.04 (−0.07, −0.01)**[b]	−0.02 (−0.05, 0.01)
Habitat	−0.09 (−0.24, 0.07)	−0.02 (−0.19, 0.15)	0.1 (−0.06, 0.26)	−0.07 (−0.24, 0.09)	−0.03 (−0.19, 0.13)
Spatial position	−0.1 (−0.27, 0.08)	−0.01 (−0.19, 0.17)	−0.07 (−0.23, 0.1)	−0.01 (−0.18, 0.17)	0.1 (−0.07, 0.27)
(4) Operationalized looking/scanning: 'Its eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with'					
Intercept	−28.35 (−28.61, −28.07)	−28.41 (−28.67, −28.14)	−28.7 (−28.94, −28.47)	−28.32 (−28.57, −28.06)	−28.76 (−28.99, −28.51)
Engaged	0 (−0.01, 0.01)	0 (−0.01, 0)	0 (−0.01, 0)	0 (−0.01, 0)	**−0.01 (−0.01, 0)**[a]
No. of neighbours	**−0.09 (−0.15, −0.04)**[c]	**−0.08 (−0.13, −0.03)**[c]	**−0.07 (−0.12, −0.01)**[c]	**−0.12 (−0.18, −0.07)**[c]	−0.04 (−0.09, 0.01)
Neighbour distance	**−0.05 (−0.07, −0.02)**[c]	**−0.03 (−0.06, 0)**[a]	−0.02 (−0.05, 0.01)	**−0.05 (−0.08, −0.02)**[c]	0 (−0.03, 0.03)
Habitat	**−0.22 (−0.37, −0.08)**[c]	**−0.16 (−0.31, −0.01)**[b]	0.03 (−0.12, 0.17)	**−0.19 (−0.34, −0.05)**[c]	−0.02 (−0.16, 0.12)
Spatial position	−0.03 (−0.17, 0.13)	−0.09 (−0.25, 0.07)	−0.04 (−0.19, 0.12)	−0.03 (−0.18, 0.12)	0.07 (−0.08, 0.22)

Each column (i.e. A.A., Observer 1. etc) represents each experienced observer; each row represents the fixed effects investigated within each observer's model. Cells are coded with asterisks according to the HDI–pd (highest density interval–probability of direction) decision rule.

[a] An effect has some uncertainty.

[b] Moderate evidence for an effect.

[c] Strong evidence for an effect. Bold cells highlight where the pd was greater than 95%.

and observers 2 and 4 produced similar findings across all models. In summary for frequency assessments, each definition produced generally varied results within observers, while there was no single definition that produced identical results across observers, even if decision rules were relaxed.

DISCUSSION

We found variation in inter-bserver agreement across four different types of vigilance definition used in primate research. When viewing results across all definitions and experienced/inexperienced observers we found excellent agreement within definition 4, operationalized looking, for both duration and frequency assessments, suggesting this definition is capturing similar information across observers. Agreement was found for other definitions in certain scenarios, but this did not carry through into frequency assessments or across the experienced/inexperienced dichotomy. Comparative model results for data produced by experienced observers suggested that each definition could lead to different results, which could vary across observers, supporting notions of definition and interpretation effects. However, definition 4 produced slightly more consistent results, with similar posterior values produced across observers for duration assessments. In general, model results for frequency assessments were more variable than for duration. Definition 4 produced very consistent estimates and HDI parameters values for three observers, but did not produce identical results across all observers, suggesting interpretation effects may be more important if frequency assessments are being investigated. Together these results suggest that while operationalized definitions produce the most consistent results for baboons, authors must take care when selecting or constructing new definitions for future work and that issues may vary according to the choice of dependent variable.

Our study set-up was designed to minimize the amount of variation that was likely to occur due to observer experience and numerous methodological factors. Observers were afforded the time to independently specify their observations with accuracy. Making similar assessments in the field using behavioural software on mobile devices or stop watches/clickers (among other methods) is likely to be less precise (and risks missing bouts entirely), with no possibility for observers to rectify accidental mistakes. The use of video-coding techniques likely plays an important role in observer interpretation of definitions and is itself vital methodological information. For example, each observer assessed numerous bouts that lasted less than half a second; this would be impossible to implement precisely in real-time/field conditions and thus would impact on how an observer interpreted and implemented a definition. Consequently, our results are at the lower end of the variation we might expect in natural settings where observers only view the behaviour once. Despite controlling for these factors, we still found variation in consistency within definitions and variation in results across definitions, suggesting there are important implications of definitions that researchers must be aware of.

Our methods controlled for other sources of variation that are likely to be important in the literature, such as variation in study species, sampling methodology (Hirschler et al., 2016), dependent variables (e.g. average bout length, interscan interval, proportion of time vigilant/looking) and statistical procedures (see supplementary material in Allan & Hill, 2018). Interactions between these factors and sampling methodology are critical as some definitions should not be possible with instantaneous point sampling; for example, definition 2 requires movement through time to be assessed. Definitions such as definition 4 may require extensive training periods to refine an observer's search images before collecting data, and, even then, assessments may be more challenging with instantaneous point sampling versus continuous or one–zero sampling. Observer fatigue is another factor we had some control over in this study as our observations were a maximum of 30 s duration and observers could take breaks as frequently as needed from video-coding. In field conditions, interpretation and definition effects may be amplified according to various challenges including focal durations, observation daylength, climatic/weather conditions, and any factors relating to the observer's own aptitude, attitude and emotional state.

We suggest researchers adopt video-sampling methods, whether recorded directly by an observer or via remote technologies such as camera traps. This should improve the precision and accuracy of observations, while offering the advantage of preserving observations, affording researchers the opportunity to apply alternative sampling methods post hoc. Videos may also be useful as new computational methods (e.g. computer tracking of head angles or line of vision) are developed, which may offer solutions to interpretation effects. In addition, videos offer authors the opportunity to monitor other observers' assessments through time to guard against interpretation and precision issues.

A limitation here may be that using ‘experienced’ observers that were familiar with different sampling methods and vigilance definitions previously could also have an important interaction with interpretation effects. Among experienced observers, agreement was excellent for definitions 1 and 4 (for the duration variable) and was approaching excellent for definition 3. Agreement was substantially lower for definitions 1 and 3 across inexperienced observers and when all observers' data were grouped. Prior experience of training, testing and observations using the definition of Treves (1998; ‘scanning/visual search directed beyond arm's reach’), may have biased experienced observers to interpret definitions 1, 3 and 4 similarly to Treves' definition, and by extension similar to one another. This seems evident as the agreement results of inexperienced observers highlighted that definition 4 was the only definition to maintain excellent agreement across all groupings, while definitions 1 and 3 achieved moderate and poor agreement, respectively. It would be interesting to explore these factors in future research as researchers who have worked on studies using certain definitions could potentially produce interpretational effects when implementing new definitions that are different to their previous work. These findings would also generalize to behaviours other than vigilance where definitions differ between studies.

Frequency assessments generally provided lower agreement, but definition 4 produced agreement estimates close to excellent regardless of how the data were grouped. These results suggest definition 4 may be somewhat more robust to prior training and experiences and could aid in making cross-study comparisons reliable. However, this may have been driven by exceptional agreement between A.A., observer 1 and observer 3, as the model estimates and HDI parameter values of their models were almost identical, while observers 2 and 4 did not share similar findings. This suggests that even when high interobserver reliability is found, minor differences in interpretation can still produce different results, which could have important implications relating to the outcome of interrater reliability/consistency tests in observational studies.

It seems likely that the definition presented by Treves (1998; ‘scanning/visual search directed beyond arm's reach’) would perform similarly to looking (4) ‘eyes are open, and its line of vision extends beyond its hands and the substrate, animal or object that they are in contact with’, in terms of interobserver agreement and consistency in results. Even so, this should be formally tested before assumptions are made, as our results suggest that even minor sources of variation can influence the direction and magnitude of results. One key difference between the two definitions is that ‘scanning (or visual search) directed beyond arm's reach’ could suggest a deliberate form of visual information acquisition, which may be interpreted as requiring some form of ‘active’ scanning. As such, observers may not all sample animals simply resting with their eyes open consistently. Over several years of training this definition with numerous observers (and primate species), A.A. found this to be a consistent source of interobserver discrepancy in interpretation, ultimately motivating the decision to present the operationalized looking definition (see Allan & Hill, 2018). The looking definition instead focuses on the animal's ‘line of vision’ as opposed to ‘scanning’ or ‘visual search’, which should allow for the unanimous inclusion of passive bouts of looking and produce more consistent data across observers than the scanning definition.

The behavioural variable (engaged/not engaged) was the only variable that could theoretically have interacted with the interpretations of each definition since certain definitions may be difficult to operationalize during engaged behaviours (e.g. foraging or grooming). However, behaviour produced fairly consistent model estimates and HDI parameter values across both duration and frequency measures suggesting that behaviour was not a primary explanation of variation in interpreting definitions across observers. As contextual variables relate to the focal animal's surrounding environment, they should not interact with the interpretation of each definition. This was supported for duration assessments regarding the spatial position variable, as model estimates and HDI parameter values were similar across definitions and observers, although the magnitude of posterior values was noticeably lower (i.e. closer to zero) for the models implemented using observer 1 and 2's duration assessments for definition 2, while observer 4 produced noticeably higher posterior values for definition 2 relative to other observers.

Results for the habitat variable were consistent for models using duration assessments, with all models accepting the null hypothesis. The null hypothesis was also accepted in all models for frequency assessments of definitions 1, 2 and 3; however, definition 4 produced evidence for an effect in three observers’ models. Results were similarly consistent for the number of neighbours and distance to nearest neighbour variables for duration assessments, with only models produced by observer 2 yielding enough evidence to potentially support an effect for definitions 1 and 2. Results were more variable for number of neighbours and distance to nearest neighbour for frequency measures. Importantly, the two social environment variables produced results that varied with respect to one another, both within observers across definitions and within definitions across observers. This is significant since each of these factors generally represents the hypotheses under investigation in vigilance studies. The latter finding also suggests that given the array of methods for sampling contextual variables in primate vigilance research (see supplementary material in Allan & Hill, 2018), consolidating towards a common method of sampling certain contextual factors may be important going forward.

We believe our results highlight a set of phenomena that are often overlooked in observational research, namely definition effects and interpretation effects. Definition effects are highlighted well with each observer producing varied results across definitions. Interpretation effects are also well supported in both our analyses. First, definitions clearly have the potential to differ in interobserver reliability and, second, it is also clear that regardless of high interobserver reliability, model estimates, HDI parameter values and ultimately the results we interpret can vary substantially not only within definitions but also across observers. Interpretation effects are most likely to manifest between independent studies using similar definitions. In these cases, differences in results could exist purely due to differences in the interpretations made by principal investigators; however, this could be further exacerbated if differences in interpretation between observers within the same study are also allowed to manifest. Studies using multiple observers during the same period can clearly control for some issues with appropriate training and testing programmes; however, we have shown here that even excellent agreement results do not guard against interpretation effects between observers within the same study. Another option may be to include observer identity in statistical analyses; however, this has rarely been used in primate vigilance research (see supplementary material in Allan & Hill, 2018) and it is unclear whether this would adequately control for interpretation effects. We kept the study species the same throughout our study, but it seems likely definition and interpretation effects would be even more problematic when applied across different species and taxa.

It seems likely that certain ethoses are more prone to within-observer variation too, that is, observers applying definitions inconsistently. We tried to avoid this source of variation in our study by actively encouraging assistants to take as much time as needed to refine their interpretations and code observations; however, most still found our set list of terms and phrases, for example head/eye angle from the ground, head/eye movement, degree of head movement, useful when formulating their initial interpretations. It is possible that this process may have introduced some bias; however, it highlighted to us that all definitions bar the operationalized looking definition were initially challenging for our observers to confidently interpret and implement without offering some advice. We suggest that future research considers avoiding defining behaviours using terms such as gazing, scanning, inspection or watchfulness, as we found these to be ambiguous and placed an onus on interpreting the internal state of an animal as opposed to assessing external markers. Our observers also found terms such as head up or side to side movement challenging to implement without further detail operationalizing when bouts begin and end; even then, assessing head angles from the ground may be challenging to reach agreement on. The looking definition circumnavigated some of these interpretation issues by asking observers to focus on the animal's line of vision in relation to their hands, which is unlikely to yield a diverse range of interpretations given its operational nature.

The operational looking definition also offers an additional advantage as it likely maximizes the amount of information collected by researchers. The behavioural markers typically used to define vigilance in nonprimate species have focused on postural changes (e.g. head raising) but some species may value visual information gained during ‘head down’ postures (Bednekoff & Blumstein, 2009; Bednekoff & Lima, 2005), while the detection capabilities of other species may not be hindered during some foraging tasks (Allan et al., 2020; Kaby & Lind, 2003). These findings highlight the issue with using postural changes as markers for vigilance and measures for fearfulness (Tatte et al., 2019) as animals can achieve vigilance goals during several postures and engaged behaviours. We believe focusing on looking (i.e. when an animal's line of vision is unobstructed and angled away from their local vicinity) is a viable solution in species where line of vision can be assessed reliably. When this is not possible authors should consider consolidating towards a key set of unambiguous markers that allow a full range of visual behaviours to be sampled. In birds, for example, the looking definition could be operationalized as any time the animal's field of view/vision is not obstructed within certain distances (e.g. a wing's length, body length or 1 m); such circumstances likely allow birds to collect information on their surrounding environment even during head down postures or during foraging. Collection of this type of information would require additional work concerning the sensory capacity of study species during a full range of postures, behaviours and scenarios (Allan & Hill, 2018). Nevertheless, it could yield a more complete understanding of how animals monitor their environment for risks. Our results highlight that sampling looking can still allow vigilance hypotheses to be tested, and risk drivers to be elucidated despite not sampling vigilance specifically.

To conclude, our findings suggest that behavioural data collection methods need to be as consistent as possible to allow for robust comparisons across study sites, species and individuals. Although we found support for the looking definition in this study, our results also indicate that very minor differences in observer interpretation can lead to varied results. Nevertheless, without convergence towards a single definition it may still be challenging to compare results both within species across populations and studies and in comparative studies across species. In baboons, we believe operational definitions are a necessity and that looking behaviours are likely to capture the most amount of information towards understanding the functions of vigilance. Operationalized looking has the potential to apply to any species with forward-facing eyes but may apply elsewhere too, particularly other catarrhine species. We encourage researchers to explore designs similar to our own in other taxa and work together to develop a more complete understanding of the extent and solutions to these issues. Even without a universal definition, it would be useful to explore and debate consolidation onto similar definitions and methods within taxonomic families and to refine the daunting list of terms and phrases currently used to define vigilance behaviours (see Allan & Hill, 2018). Ultimately, we hope our results are useful in instigating a wider debate among behavioural ecologists about definitions and sampling design for all behaviours, not just vigilance.

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References

Alberts, S. C. (1994). Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. *Animal Behaviour, 47*(4), 749–755.

Allan, A. T. L., Bailey, A. L., & Hill, R. A. (2020). Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Science Advances, 6*, eaaz0870.

Allan, A. T. L., & Hill, R. A. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. *American Journal of Physical Anthropology, 165*, 4–22.

Arenz, C., & Leger, D. (2000). Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour, 59*(3), 535–541.

Atkins, A., Little, R. M., Redpath, S. M., & Amar, A. (2019). Impact of increased predation risk on vigilance behaviour in a gregarious waterfowl, the Egyptian goose *Alopochen aegyptiaca*. *Journal of Avian Biology, 50*(e02121), 1–8.

Barros, M., Alencar, C., Silva, M. A. de S., & Tomaz, C. (2008). Changes in experimental conditions alter anti-predator vigilance and sequence predictability in captive marmosets. *Behavioural Processes, 77*(3), 351–356.

Beauchamp, G. (2015). *Animal vigilance: monitoring predators and competitors*. Academic Press.

Beauchamp, G. (2017). What can vigilance tell us about fear. *Animal Sentience, 15*(1), 1–53.

Beauchamp, G. (2018). The effect of age on vigilance: A longitudinal study with a precocial species. *Behaviour, 155*(13), 1011–1024.

Bednekoff, P. A., & Blumstein, D. T. (2009). Peripheral obstructions influence marmot vigilance : Integrating observational and experimental results. *Behavioral Ecology, 20*, 1111–1117.

Bednekoff, P. A., & Lima, S. L. (2005). Testing for peripheral vigilance: Do birds value what they see when not overtly vigilant? *Animal Behaviour, 69*(5), 1165–1171.

Blumstein, D. T., Lea, A. J., Olson, L. E., & Martin, J. G. A. (2010). Heritability of anti-predatory traits : Vigilance and locomotor performance in marmots. *Journal of Evolutionary Biology, 23*, 879–887.

Boinski, S. U. E., Kauffman, L., Westoll, A., Stickler, C. M., Cropp, S., & Ehmke, E. (2003). Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis, S. sciureus*). *Behaviour, 139*, 1421–1467.

Brandl, S. J., & Bellwood, D. R. (2015). Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. *Scientific Reports, 5*(14556), 1–13.

Brown, N. A., Ruckstuhl, K. E., Donelon, S., & Corbett, C. (2010). Changes in vigilance, grazing behaviour and spatial distribution of bighorn sheep due to cattle presence in Sheep River Provincial Park, Alberta. *Agriculture, Ecosystems & Environment, 135*, 226–231.

Burger, J., & Gochfeld, M. (1988). Effects of group size and sex on vigilance in ostriches (*Stuthio camelus*): Antipredator strategy or mate competition? *Ostrich - Journal of African Ornithology, 59*(1), 14–20.

Bürkner, P.-C. (2017). brms : An R package for bayesian multilevel models using stan. *Journal of Statistical Software, 80*(1), 1–28.

Campos, F. A., & Fedigan, L. M. (2014). Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology, 25*(3), 477–486.

Carrasco, J. L., & Jover, L. (2003). Estimating the generalized concordance correlation coefficient through variance components. *Biometrics, 59*, 849–858.

Carrasco, J. L., & Martinez, J. P. (2015). Package ‘ cccrm’. https://cran.r-project.org/package=cccrm.

Carrasco, J. L., Phillips, B. R., Puig-Martinez, J., King, T. S., & Chinchilli, V. M. (2013). Estimation of the concordance correlation coefficient for repeated measures using SAS and R. *Computer Methods and Programs in Biomedicine, 109*, 293–304.

Carter, A. J., Pays, O., & Goldizen, A. W. (2009). Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. *Behavioral Ecology and Sociobiology, 64*(2), 237–245.

Chen, C., & Barnhart, H. X. (2013). Assessing agreement with intraclass correlation coefficient and concordance correlation coefficient for data with repeated measures. *Computational Statistics & Data Analysis, 60*, 132–145.

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour, 88*, 165–173.

Cowlishaw, G. (1998). The role of vigilance in the survival and reproductive strategies of Desert Baboons. *Behaviour, 135*(4), 431–452.

Cowlishaw, G., Lawes, M. J., Lightbody, M., Martin, A., Pettifor, R., & Rowcliffe, J. M. (2004). A simple rule for the costs of vigilance: Empirical evidence from a social forager. *Proceedings of the Royal Society B: Biological Sciences, 271*(1534), 27–33.

Duane, S., Kennedy, A. D., Pendleton, B. J., & Roweth, D. (1987). Hybrid Monte Carlo. *Physics Letters B, 195*(2), 216–222.

Elgar, M. A., & Catterall, C. P. (1981). Flocking and predator surveillance in house sparrows: Test of an hypothesis. *Animal Behaviour, 29*(3), 868–872.

Favreau, F.-R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society B, 277*, 2089–2095.

Fernandez, G. J., Capurro, A. F., & Reboreda, J. C. (2003). Effect of group size on individual and collective vigilance in greater rheas. *Ethology, 109*, 413–426.

Ferrari, C., Bogliani, G., & von Hardenberg, A. (2009). Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surrounding. *Ethology Ecology & Evolution, 21*, 355–364.

Forslund, P. (1993). Vigilance in relation to brood size and predator abundance in the barnacle goose, *Branta leucopsis*. *Animal Behaviour, 45*(5), 965–973.

Fragaszy, D. (1990). Sex and age differences in the organisation of behaviour in wedge-capped capuchins, *Cebus olivaceus*. *Behavioral Ecology, 1*(1), 81–94.

Gaynor, K. M., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour, 84*(3), 531–537.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science, 7*(4), 457–472.

Hallgren, K. A. (2012). Computing inter-rater reliability for observational data: An overview and tutorial. *Tutorials in Quantitative Methods for Psychology, 8*(1), 23–34.

Hernaez, R. (2015). Reliability and agreement studies: A guide for clinical investigators. *Gut, 64*(7), 1018–1027.

Hill, R. A., & Cowlishaw, G. (2002). Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations. In L. E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 187–204). Cambridge University Press.

Hirschler, I. M., Gedert, J. L., Majors, J., Townsend, T., & Hoogland, J. L. (2016). What is the best way to estimate vigilance? A comparison of two methods for gunnison's prairie dogs, *Cynomys gunnisoni*. *Animal Behaviour, 121*, 117–122.

Hoffman, M. D., & Gelman, A. (2014). The No-U-turn sampler: Adaptively setting path lengths in Hamiltonian Monte Carlo. *Journal of Machine Learning Research, 15*, 1593–1623.

Ito, R., & Mori, A. (2010). Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (*Reptilia: Iguania*). *Proceedings of the Royal Society B, 277*, 1275–1280.

Javier, D.-R. F., & Perez-Mellado, V. (2000). The effects of population density on time budgets of the iberian wall lizard (*Podarcis hispanica*). *Israel Journal of Zoology, 46*, 215–229.

Kaby, U., & Lind, J. (2003). What limits predator detection in blue tits (*Parus caeruleus*): Posture, task or orientation? *Behavioral Ecology and Sociobiology, 54*, 534–538.

Kahlert, J. (2003). The constraint on habitat use in wing-moulting Greylag Geese *Anser anser* caused by anti-predator displacements. *Ibis, 145*, E45–E52.

Klett-mingo, J. I., Pavon, I., & Gil, D. (2016). Great tits, Parus major, increase vigilance time and reduce feeding effort during peaks of aircraft noise. *Animal Behaviour, 115*, 29–34.

Koo, T. K., & Li, M. Y. (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of Chiropractic Medicine, 15*(2), 155–163.

Kruschke, J. K. (2018). Rejecting or accepting parameter values in bayesian estimation. *Advances in Methods and Practices in Psychological Science, 1–11*.

Kruschke, J. K., & Liddell, T. M. (2018). Bayesian data analysis for newcomers. *Psychonomic Bulletin & Review, 25*, 155–177.

Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology, 112*(6), 581–591.

Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. *International Journal of Primatology, 28*(4), 907–918.

Lanham, E. J., & Bull, C. M. (2004). Enhanced vigilance in groups in *Egernia stokesii*, a lizard with stable social aggregations. *Journal of Zoology, 263*, 95–99.

Lian, X., Zhang, T., Cao, Y., Su, J., & Thirgood, S. (2007). Group size effects on foraging and vigilance in migratory Tibetan antelope. *Behavioural Processes, 76*, 192–197.

Li, D., Liu, Y., Sun, X., Lloyd, H., Zhu, S., Zhang, S., & Wan, D. (2017). Habitat-dependent changes in vigilance behaviour of Red-crowned Crane influenced by wildlife tourism. *Scientific Reports, 7*(16614), 1–11.

Lopez, P., & Martin, J. (2013). Effects of microhabitat-dependent predation risk on vigilance during intermittent locomotion in Psammodromus algirus lizards. *Ethology, 119*, 316–324.

MacIntosh, A. J. J., & Sicotte, P. (2009). Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): An examination of the effects of conspecific threat and predation. *American Journal of Primatology, 71*(11), 919–927.

Makowski, D., Ben-Shachar, M. S., Chen, S. H. A., & Ludecke, D. (2019). Indices of effect existence and significance in the bayesian framework. *Frontiers in Psychology, 10*, 2767.

McElreath, R. (2019). *Statistical rethinking 2: A Bayesian course with examples in R and Stan* (2nd ed.). Chapman and Hall/CRC.

McVean, A., & Haddlesey, P. (1980). Vigilance schedules among house sparrows *Passer domesticus*. *Ibis, 122*, 533–536.

Neal, R. M. (2003). Slice sampling: Rejoinder. *Annals of Statistics, 31*(3), 705–767.

Nunes, D. M., Gonçalves, I., Emile, N., & Barros, M. (2010). Bimodal temporal organization of specific vigilance behaviors in captive black tufted-ear marmosets (*Callithrix penicillata*). *Behavioural Processes, 84*(2), 629–631.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology, 38*, 419–422.

Quenette, P. (1990). Functions of vigilance behavior in mammals: A review. *Acta Oecologica, 11*(6), 801–818.

Quirici, V., Castro, R. A., Oyarzún, J., & Ebensperger, L. A. (2008). Female degus (*Octodon degus*) monitor their environment while foraging socially. *Animal Cognition, 11*(3), 441–448.

R Core Team. (2018). *Rtools software, Version 35*. R Foundation for Statistical Computing.

R Core Team. (2019). *R: A language and environment for statistical computing. Version 3.6.1*. R Foundation for Statistical Computing.

Rieucau, G., & Martin, J. G. A. (2008). Many eyes or many ewes: Vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. *Oikos, 117*, 501–506.

de Ruiter, J. R. (1986). The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour, 98*(1), 240–258.

van Shaik, C., & van Noordwijk, M. (1989). The special role of male Cebus monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology, 24*(5), 265–276.

Shimada, T., & Shimada, K. (2003). Factors affecting vigilance in greater white-fronted geese *Anser albifrons*. *Wildfowl, 54*, 201–208.

Shriner, W. M. (1998). Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Animal Behaviour, 55*, 529–536.

Smith, A. C., Kelez, S., & Buchanan-Smith, H. M. (2004). Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). *Behavioral Ecology and Sociobiology, 56*(1), 18–25.

Stan Development Team. (2019). RStan: the R interface to Stan. R package version 2.21. 2. http://mc-stan.org/.

Stojan-Dolar, M., & Heymann, E. W. (2010). Vigilance in a cooperatively breeding primate. *International Journal of Primatology, 31*(1), 95–116.

Tadeo, M. P., & Gammell, M. (2018). Activity budgets in different habitats of a species of conservation concern in Ireland, the Light-bellied Brent Goose *Branta bernicla hrota*. *Wildfowl, 68*, 84–103.

Tatte, K., Ibanez-Alamo, J. D., Marko, G., Mand, R., & Moller, A. P. (2019). Antipredator function of vigilance re-examined: Vigilant birds delay escape. *Animal Behaviour, 156*, 97–110.

Teichroeb, J. A. (2017). Methodological suggestions for inferring fear from vigilance. *Animal Sentience, 15*(6), 1–2.

Treves, A. (1998). The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour, 135*(4), 453–481.

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology, 48*(2), 113–126.

Treves, A., Drescher, A., & Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology, 50*(1), 90–95.

Treves, A., Drescher, A., & Snowdon, C. T. (2003). Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology, 109*(2), 135–146.

Unck, C. E., Waterman, J. M., Verburgt, L., & Bateman, P. W. (2009). Quantity versus quality: How does level of predation threat affect cape ground squirrel vigilance? *Animal Behaviour, 78*, 625–632.

Vasquez, R. A. (1997). Vigilance and social foraging in *Octodon degus* (*rodentia: Octodontidae*) in central Chile. *Revista Chilena de Historia Natural, 70*, 557–563.

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology, 90*(2), 546–555.

Williams, S. T., Williams, K. S., Lewis, B. P., & Hill, R. A. (2017). Population dynamics and threats to an apex predator outside protected areas: Implications for carnivore management. *Royal Society Open Science, 4*, 161090.

Yaber, M. C., & Herrera, E. A. (1994). Vigilance, group size and social status in capybaras. *Animal Behaviour, 48*, 1301–1307.

Chapter 4. Investigating whether the outcome of habituation processes renders researchers a neutral stimulus to study subjects, and whether the outcome is equal across all group members.

Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait

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AA conceived and coordinated the study, collected field data, carried out statistical analysis, and drafted the initial manuscript. AB collected field data, participated in statistical analysis, and critically revised the manuscript. RH participated in study design, statistical analysis and critically revised the manuscript.

ECOLOGY

Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait

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In behavioral studies, observer effects can be substantial, even for habituated animals, but few studies account for potential observer-related phenomenon empirically. We used wild, habituated chacma baboons to explore two key assumptions of behavioral ecology (i) that observers become a "neutral" stimulus and (ii) that habituation is "equal" across group members. Using flight initiation distance (FID) methods within a personality paradigm, the behavioral responses of baboons suggested that observers were not perceived as neutral but instead viewed as a high-ranking social threat. Habituation was also not equal across group members, with repeatable individual differences more important than contextual factors (e.g., habitat) in determining the distance at which baboons visually oriented or displaced from observers. A strong correlation between individual visual tolerance and displacement tolerance (i.e., convergent validity) indicated a personality trait. We offer several suggestions for how to account for these factors and minimize potential bias in future studies.

INTRODUCTION

Habituation has been referred to as "a process that leads to decreased responsiveness to a stimulus" [see page 255 of (*1*)]. In behavioral ecology, habituation has been used to reduce the risk perception that wild animals have toward human observers, with the outcome of such processes or "full habituation" described as "individual accepts humans (and apparently ignores them) at close range during all activities; they appear calm when they are alone with humans and are relatively easy to follow while travelling" [see page 164 of (*2*)]. This allows researchers to conduct behavioral observations under the assumption that study subjects have lost their fear of human observers and view them as a neutral stimulus (*3*, *4*). The wealth of literature using data collected from behavioral observations on habituated animals suggests that this process is tried and tested in numerous species. However, recent work strongly suggests that observer presence is unlikely to have a neutral effect on study animals. Welch and colleagues (*5*) found that bat-eared foxes (*Otocyon megalotis*) increased vigilance during the early stages of focal observations, while reef fishes had significantly higher rates of cleaning interactions when data were collected using video observations (divers absent) versus direct observations by divers (*6*). Nevertheless, while the concept of observer neutrality has received discussion across a range of species typically exposed to direct observations [e.g., baboons (*7*), macaques (*8*), bonobos (*9*), and meerkats (*10*)], overall, there is a lack of empirical research focusing on observer neutrality in habituated systems.

The outcome of habituation processes has been referred to as tolerance, with highly tolerant animals consistently allowing closer approaches by humans without adjusting their behavior or fleeing and vice versa for highly intolerant animals (*1*). This suggests that the tolerance outcome of habituation processes exists along a spectrum, allowing tolerance to vary across individuals, groups, and species. Hanson and Riley (*8*) highlighted an observable difference in tolerance across two study groups of moor macaques (*Macaca maura*), further suggesting that habituation is a flexible, context-dependent spectrum of heightened observer tolerance. Beyond group or species differences in tolerance, the wider assumption that the outcome of habituation can be considered "equal" across individuals within groups (and across solitary individuals) remains untested empirically. If subtle variation in tolerance levels is overlooked, then a key driver of behavioral patterns is also missed, which could have far-reaching implications for behavioral research.

If there are consistent interindividual differences in tolerance to human observers and within-individual tolerance is consistent through time and in response to multiple contexts and situations, then tolerance would satisfy the conditions for being classed as a personality trait (*11*). If tolerance is a personality trait, then it suggests that three implicit assumptions concerning habituated animals may not be entirely valid, namely, (i) that observers are considered neutral, (ii) that habituation (i.e., tolerance) is equal across study animals, and (iii) that observers play little to no role in the behaviors that they record. Here, we explore these assumptions within a tolerance-personality paradigm using a group of Afromontane chacma baboons (*Papio ursinus griseipes*) as a model species.

As individual tolerance has yet to receive attention from a personality perspective, identifying an ecologically valid measure is of critical importance. The factors influencing the habituation process have received some attention in primatology (*12*). Behaviors such as observer-directed aggression (*13*) and self-directed behaviors (*14*) were both found to decrease over the course of habituation in white-headed capuchins (*Cebus capucinus*) and vervet monkeys (*Chlorocebus pygerythrus*), respectively. Baboons (*Papio* spp.) and rhesus macaques (*Macaca mulatta*) were shown to exhibit altered behavioral patterns between observer presence and absence treatments, but effects differed across species and sex (*15*). In contrast, there was no evidence found that observer presence influenced the activity patterns, ranging behavior, or proximity to neighboring conspecific groups of wild habituated white-faced capuchins (*C. capucinus*) (*16*). While understanding the habituation process and behavior in the presence/absence

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of observers is important, the approach does not offer a methodological framework to assess any individual personality factors relating to tolerance to observers or the real-time implications of human presence on the behavior of study animals.

Personality types in wild habituated baboons (*Papio ursinus ruacana*), specifically boldness and anxiousness, have been demonstrated in response to novel food items and model predators, respectively (*17*). Both traits were investigated using both categorical/binary responses (e.g., back away or tail flag) and continuous measures (e.g., handling time) under experimental conditions (*17*), with each process relying on individuals encountering and responding to static stimuli. However, tolerance centers around an individual's tendency to endure the behavior of a human observer without altering behavioral patterns, and as a result, static stimuli are inappropriate. Instead, measures need to mimic the stimuli of human observers moving around the environment concurrent to study animals (*18*).

Quantitative and objective measures are thus required to infer tolerance (*8*). Flight initiation and alert distances offer a methodological process that produces continuous measures (i.e., distance) in response to an observer walking toward study animals (*19*). Optimal escape theory predicts that the point at which prey decides to flee from an approaching predator, otherwise known as flight initiation distance (FID), is governed by a trade-off between the risk of being predated upon and the benefits of staying to engage in any fitness-enhancing activity; increasing perceived risk of predation should thus lead to increased FID (*20*, *21*). FID methodology has previously been used as a proxy for measuring the personality trait boldness (*22*, *23*), in each case assessing individual repeatability in FID responses as a proxy for the boldness trait. Inferring boldness using FID methodology is dependent on the assumption that human approachers are considered threatening or novel, but FID approaches on habituated animals are unlikely to be an ecologically valid measure of an animal's propensity to engage in risky, innovative, or novel behaviors (i.e., boldness). Instead, it is likely to measure the propensity of individuals to endure human actions without altering behavior (i.e., tolerance). A clear tolerance measure that can be derived from FIDs is "displacement tolerance," the propensity of an animal to endure proximity to a human observer without moving away. Tied to this is the additional measure of "detection distance" that should also provide an ecologically valid method for inferring visual tolerance, i.e., individual tendency to visually orient or to resist directing looking toward an approaching observer.

In this study, we used FID methodology to explore whether tolerance can be considered a personality trait in Afromontane chacma baboons exploring individual repeatability for two specific behaviors: FID and visual orientation distance (VOD). FID refers to the distance at which individual baboons were displaced by approaching humans (Fig. 1), while VOD refers to the distance at which individual baboons oriented their looking behavior toward the observer as a result of their approach. Typically, FID studies will record a vigilance or alert distance (*19*). We use VOD as an equivalent for alert distance; the difference in terminology is based on the constraint that this study focuses on habituated primates that are aware of our presence before initiating approaches, and so, visual orientation, as opposed to alert, best describes the behavior of the focal animal looking toward the approaching observer.

To be considered a personality trait, the two measures of tolerance (FID and VOD) need to be consistent within individuals and distinct between individuals across multiple contexts through time (*11*). To explore this, we exposed individual baboons to repeated trials in a range of environmental and social contexts (see contextual variables in Table 1) using two different observers varying in familiarity to the baboons. This setup allowed robust investigation into the tolerance personality trait hypothesis and generated two initial predictions: Environmental, social, methodological, and observer factors should play a minimal role in VOD and FID, i.e., individual baboon identity should account for a larger degree of the variance in FID and VOD (prediction 1), and individuals are consistent in both their FID and VOD responses to an approaching observer through time, i.e., individual repeatability (prediction 2). We explored the factors influencing VOD and FID separately using a Bayesian mixed-model approach. The final aspect of the tolerance personality hypothesis was to test for convergent validity [see (*24*)], through the correlation between displacement tolerance (derived from individual FID) and visual tolerance (derived from individual VOD). We predicted that visual tolerance and displacement tolerance would be correlated, such that both measure the same trait (prediction 3). This was explored using bivariate Bayesian mixed model analysis (*25*), retaining the predictors from the analyses for predictions 1 and 2.

RESULTS

Perceived threat level of approaching observers

We completed 1656 trials across 69 individual baboons (24 trials each; table S3), with behavioral responses recorded to understand the perceived threat level observers represented (Table 2). Observers do not appear to be considered equivalent to a predator. Instead, baboon responses mimic typical responses to approaches from dominant or threatening conspecifics. This suggests that observers are unlikely

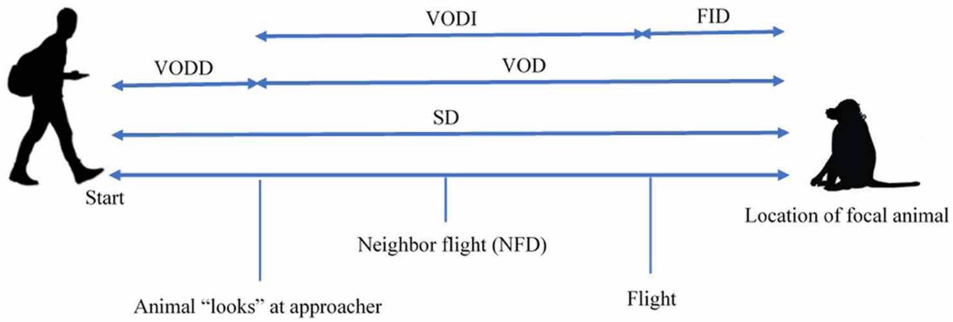

Fig. 1. FID procedure and measurements. This highlights the distance variables that can be measured as a function of the focal animal's behavioral responses. Start distance (SD), visual orientation distance (VOD), VOD delay (VODD), VOD interval (VODI), flight initiation distance (FID). Adapted from (*57*).

Table 1. Factors hypothesized to influence VOD and FID in baboons. Contextual variables that could be major drivers of VOD and FID responses in habituated chacma baboons (examples from relevant literature supporting the inclusion of each hypothesis can be found in table S1).

Factors	Link to sensory capacity/FID/personality
Response variable: VOD	
Observer (pseudo-predator) identity, X_1	Unfamiliar observer considered a greater threat, leading to increased risk perception and tendency to visually orient, resulting in longer VOD
Trial number, X_2	(i) Increase or decrease in VOD with trial number indicative of habituation or sensitization (respectively) to FID approach methodology
	(ii) Consistent individual VOD response through time indicates personality trait.
Compatibility: Not engaged (looking/not looking), engaged (not looking), X_3	Looking may enable animals to collect multiple types of information concurrently; in addition, being “not engaged” may afford focal animals a greater sensory capacity for detection. As a result, individuals looking as approach commences will visually orient toward approaching observer sooner resulting in longer VOD; engaged should yield shorter VOD.
Habitat (open/closed), X_4	(i) “Open” habitats may afford individuals greater visibility, increasing likelihood of attending to approaching observer quicker, resulting in longer VOD.
	(ii) Open habitats are generally considered safer for baboons, as they permit earlier detection and avoidance of predators; therefore, risk perception could be lower, reducing tendency to visually orient toward approaching observer, resulting in shorter VOD.
	(iii) Open habitats may increase risk perception, as focal animals are less concealed from potential threats, increasing tendency to visually orient toward approaching observer, resulting in longer VOD.
	(iv) Open habitats have lower refuge availability, which may increase risk perception, resulting in longer VOD.
Height (ground/above ground), X_5	“Above ground” may afford individuals greater visibility, resulting in longer VOD. In this context, above ground is <50 cm from ground level and is unlikely to qualify as potential refuge and therefore should not influence risk perception.
Number of neighbors within 5 m, X_6	(i) As number of neighbors increase, the likelihood of a neighbor visually orienting toward the approacher increases, i.e., collective detection, which could result in longer VOD.
	(ii) As number of neighbors increase, the likelihood of predation decreases reducing risk perception and the tendency to visually orient toward the approach observer, resulting in shorter VOD.
	(iii) Increasing number of neighbors may mask both the visual and audible cues associated with the observer’s approach, resulting in shorter VOD, e.g., neighbors draw visual attention away from observer or noises from neighbors mask the sounds of observer’s footsteps during approach.
Neighbor flight, X_7	Local conspecifics initiating flight before the focal animal will increase risk perception and evoke vigilance. Both factors could lead to focal animals visually orienting toward approaching observer sooner, resulting in longer VOD.
External factors (local alarms, aggressions within 5 min), X_8	Localized threatening stimuli lead to increased risk perception and tendency to visually orient, resulting in longer VOD.
	Localized visual and audible stimuli may reallocate some of the focal animal’s finite attention, resulting in longer VOD.
Response variable: FID	
VODI, X_9	When visual orientation interval (distance between VOD and FID) is long, focal animals will flee sooner, resulting in longer FID.
Engaged/Not engaged, X_{10}	FID will be higher if focal animal was engaged at the start of the approach, as flight costs are higher because of interrupted social time (i.e., grooming) or loss of food patch (i.e., foraging).
Observer (pseudo-predator) identity, X_1	Unfamiliar observer is considered a greater threat; therefore, FID should be greater for unfamiliar observer

continued to next page

Factors	Link to sensory capacity/FID/personality
Trial number, X_2	(i) Increase or decrease in FID with trial number indicative of sensitization or habituation (respectively) to FID approach methodology
	(ii) Consistent FID response through time indicates personality trait.
Habitat (open/closed), X_4	(i) Open habitats are generally considered safer for baboons, as they permit earlier detection and avoidance of predators; therefore, risk perception could be lower, resulting in shorter FID.
	(ii) Open habitats may increase risk perception, as focal animals are less concealed from potential threats, resulting in longer FID.
	(iii) Open habitats have lower refuge availability, which may increase risk perception, resulting in longer FID.
Number of neighbors within 5 m, X_6	(i) Risk diluted with greater number of neighbors; therefore, FID should decrease as number of neighbors increases.
	(ii) Increasing number of neighbors increases localized visual and audible stimuli and therefore may reallocate some of the focal animal's finite attention resulting in decreased FID.
Neighbor flight, X_7	Local conspecifics initiating flight before the focal animal will increase risk perception and therefore increase FID.
External factors (local alarms, aggressions within 5 min), X_8	(i) Localized threatening stimuli leads to increased risk perception and therefore increased FID.
	(ii) Localized visual and audible stimuli may reallocate some of the focal animal's finite attention therefore decreasing FID.

to be considered "neutral" but are instead more equivalent to a high-ranking social threat.

VOD model

We implemented a maximal (or "global") model containing all of our predictors of VOD with results suggesting that the compatibility, habitat, and number of neighbors variables were the most informative covariate predictors for VOD, with the envelope constraint well controlled for [Table 3: VOD delay (VODD) estimate = −0.02, Rhat = 1.00]. Compatibility variables seem to have a consistent influence on VOD, with longer VOD (earlier detection) for both looking and not engaged not looking categories compared to animals that were fully engaged, although the mean conditional effect estimates of engaged and looking differed by only 60 cm, suggesting that the detection capabilities of baboons may not be completely limited when not looking or when performing engaged behaviors. Animals in open habitats also detected observers sooner (longer VOD), although the effect was not as strong as the compatibility variables. Number of neighbors had a small negative estimate, but its credible intervals did not overlap zero, suggesting weak yet consistent effect. VOD was also longer (earlier orientation) when neighbors fled before the focal animal, although credible intervals included zero. The remaining covariates did not appear to add considerable explanatory power to predicting VOD, as each had estimates close to zero and credible intervals overlapping zero (see Table 3).

FID model

The maximal model for FID revealed that the engaged, habitat, and number of neighbors variables were the most informative covariate predictors for FID. The model results suggest that the envelope constraint was well controlled for [Table 4: VOD interval (VODI) estimate = −0.04, Rhat = 1.00] but provide little support for the Flee Early and Avoid the Rush (F.E.A.R.) hypothesis (*26*) (see Table 1: X_9), as a minor negative estimate was produced for VODI with credible intervals both close to zero (Table 4). Animals that were not engaged at the start of an approach have longer FIDs (i.e., displace sooner), with animals in open habitats also appearing to displace earlier, resulting in longer FIDs. Animals that were on the ground throughout the approach had longer FIDs than animals slightly above the ground, although credible intervals included zero. Number of neighbors produced a consistent (narrow credible intervals) but weak negative effect. The effect of the unfamiliar observer produced a weak negative estimate, but credible intervals overlapped zero, suggesting little confidence in this factor being an important driver of FID. The remaining covariates did not appear to add considerable explanatory power to predicting FID, as each had estimates close to zero and credible intervals overlapping zero (see Table 4).

These results mimic those found for VOD, with little suggestion that habituation/sensitization to methodological stimulus took place. In addition, little difference was found between observers (for VOD or FID), both in absolute terms and in their individual effect over the course of successive trials (see Tables 3 and 4 and Fig. 2). For both FID and VOD, the "unfamiliar" observer produced consistent estimates through successive trials. The baboons' responses to a "familiar" observer (AA) produced a declining trend for both VOD and FID, suggesting that study animals were initially sensitive to the approaches of AA but slightly habituated over the course of successive trials (Fig. 2); however, the effect did not carry sufficient statistical weight. The study group's prior experience of being observed by AA may suggest that actions of an observer outside of their "normal" behavior (i.e., the repeated direct FID approaches) were considered somewhat threatening to baboons, but the declining trend also suggests that the study group as a whole adapted and habituated to this unusual behavior quite quickly.

Table 2. Responses by baboons to approach and hypothesized meaning. Hypothesized individual baboon behavioral response to human approaches and the threat level these responses are considered equivalent to.

Observer considered:	Equivalent to predator	Equivalent to social threat	Minimal threat	No threat	No. of observations (percentage of total observations)
Response predictor					
Alarm bark	Y	–	–	–	0 (0%)
Flight direct to refuge (rocks, trees, or cliff)	Y	–	–	–	0 (0%)
Rapid flight/sprinting response	Y	Y	–	–	0 (0%)
Displacement with geck/grimace	–	Y	–	–	16 (0.97%)
Animal passively displaces	–	Y	Y	–	1637 (98.85%)
Flinch/startled before flight*	–/*	–/*	–/*	–/*	3 (0.18%)
Animal is not displaced	–	–/*	–	Y	0 (0%)
Animal is not displaced and threatens observer	–	–	–	Y	0 (0%)

*Flinch or startled suggests that the focal animal detected observer within its usual tolerance level.

Tolerance as a personality trait

To test whether visual tolerance (VOD) and displacement tolerance (FID) were distinct among individuals, we removed the individual identity random effect from each model and used log-score stacking [see (*27*)] to combine its Bayesian predictive distribution with the same model inclusive of individual identity. For both the VOD and FID, removal of the individual identity random effect resulted in a less informative model with log-score stacking favoring the inclusion of individual identity in both cases: VOD model with individual identity weight, 0.987; model without individual identity weight, 0.013; FID model with individual identity weight, 0.999; and model without individual identity weight, 0.001. In addition, parameter estimates and credible intervals from each model suggested that individual identity was a key predictor of VOD and FID [see sd (intercept) in Tables 3 and 4]. In both cases, estimates for ID were greater than each of the covariate predictors, while credible interval did not overlap zero. These results strongly suggest that individual identity was the most important driver of VOD and FID, emphasizing that both measures are distinct among individuals.

To test whether VOD and FID were consistent within individuals, we calculated the intraclass correlation coefficient (ICC) from the univariate VOD and FID models using an enhanced agreement repeatability protocol (see the "Statistical analysis" section for description) (*28*). We observed moderate ICC estimates for individual identity in both VOD (individual identity ICC, 0.38; highest density intervals (HDI) for posterior samples at 95% intervals, 0.24, 0.51) and FID (individual identity ICC, 0.65; HDI, 0.56, 0.74) after accounting for variance explained by fixed effects and observation date. Following Houslay and Wilson (*25*), we used the above protocol to also derive ICC calculations from a bivariate model (see below) for both VOD (ICC, 0.38; HDI, 0.27, 0.50) and FID (ICC, 0.62; HDI, 0.54, 0.74), each producing almost identical values to the univariate approach. In each case, the lower bound of the Bayesian 95% credible interval was not close to zero, indicating that there is at least moderate confidence in a nonzero proportion of phenotypic variance in both VOD and FID being explained by within-individual consistency (*25*). While these ICC estimates may be considered "moderate" (*29*), personality analyses have previously interpreted values as low as 0.168 to be suggestive of repeatability (*23*), with 0.342 reflecting repeatability in male reindeer (*30*), suggesting that both the visual and displacement responses of this baboon group have a clear personality component. These findings are strong evidence that both tolerance behaviors were consistent within, and distinct among individuals, and were therefore taken to indicate that the behaviors manifest themselves as a personality trait (*31*).

Convergent validity

We followed (*25*) and implemented a bivariate Bayesian model to assess convergent validity, with VOD and FID included as response variables and each predicted by the same covariates used in the maximal models. We used the same priors, random structure, and log-normal response distribution, as used in univariate models. After fitting this model, we estimated the mean and credible intervals of the correlation between VOD and FID from the bivariate model covariances. A new posterior distribution was constructed from the among-individual correlation by dividing the covariance between VOD and FID by the product of the square root of their individual trait variances, thus standardizing their covariances on a scale from −1 to 1. This process produced a mean correlation of 0.875 between visual tolerance (VOD) and displacement tolerance (FID), with a lower high-density credible interval of 0.767 and a higher HDI of 0.967, suggesting a very high degree of confidence in concluding a statistically significant correlation and thus meeting the requirement for convergent validity (*25*).

Table 3. VOD model summary. Parameter estimates for the model describing the relationship between VOD and the predictor variables. CI, credible interval.

Population-level effects

	Estimate	Est. error	1–95% CI	U-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.06	0.08	0.9	1.22	1.00	23,289	35,333
VODD	–0.02	0.01	–0.03	0	1.00	34,760	41,624
Looking	0.21	0.02	0.17	0.25	1.00	69,337	46,658
Not engaged not looking	0.11	0.02	0.06	0.16	1.00	70,821	47,802
Open (Habitat)	0.15	0.02	0.12	0.19	1.00	73,748	46,813
Ground (Height)	0.06	0.05	–0.04	0.16	1.00	74,865	45,743
Number of neighbors	–0.05	0.01	–0.06	–0.03	1.00	76,910	46,466
Neighbor flee first	0.08	0.04	0	0.16	1.00	78,003	46,586
External factors within 5 min	0.02	0.03	–0.04	0.08	1.00	79,045	47,160
Unfamiliar observer (AB)	–0.04	0.07	–0.19	0.11	1.00	17,011	28,032
Trial number	–0.01	0.01	–0.02	0.01	1.00	18,351	29,277
Unfamiliar observer (AB): Trial number	0.01	0.01	–0.01	0.03	1.00	17,138	26,376
Family specific (log-normal)							
Sigma	0.31	0.01	0.3	0.32	1.00	48,397	43,998
Group-level effects							
Date (58 levels)							
sd(Intercept)	0.14	0.02	0.1	0.18	1.00	17,027	32,825
Individual identity (69 levels)							
sd(Intercept)	0.24	0.03	0.18	0.31	1.00	13,558	27,638
sd(VODD)	0.04	0.01	0.02	0.05	1.00	19,663	31,617
sd(ObserverAB)	0.09	0.04	0.01	0.17	1.00	7,956	13,090
sd(TrialNo)	0.01	0	0	0.02	1.00	7,995	11,891
sd(ObserverAB:TrialNo)	0.01	0.01	0	0.02	1.00	5,454	12,200
cor(Intercept,VODD)	0.57	0.19	0.15	0.89	1.00	14,071	24,184
cor(Intercept,ObserverAB)	0.21	0.31	–0.46	0.76	1.00	25,091	33,269
cor(VODD,ObserverAB)	0.16	0.33	–0.53	0.74	1.00	20,671	33,171
cor(Intercept,TrialNo)	–0.68	0.22	–0.94	–0.1	1.00	22,289	21,411
cor(VODD,TrialNo)	–0.3	0.29	–0.8	0.32	1.00	17,875	27,326
cor(ObserverAB,TrialNo)	–0.17	0.37	–0.81	0.57	1.00	17,569	30,321
cor(Intercept,ObserverAB:TrialNo)	0.35	0.3	–0.37	0.82	1.00	18,449	21,803
cor(VODD,ObserverAB:TrialNo)	0.29	0.31	–0.41	0.8	1.00	27,315	29,181
cor(ObserverAB,ObserverAB:TrialNo)	–0.05	0.39	–0.72	0.72	1.00	17,705	33,765
cor(TrialNo,ObserverAB:TrialNo)	–0.47	0.34	–0.91	0.4	1.00	9,755	21,676

We additionally extracted the conditional modes (posterior modes) of each individual baboon for both VOD and FID (see Fig. 3). Conditional modes are the equivalent of best linear unbiased predictors, which have been used elsewhere in personality research [e.g., (*22*, *25*)]. Conditional modes terminology reflects the fact that the computation works to maximize the density of the individual identity random effect conditioned on the variance-covariance matrix of the fitted model framework and observed data (*32*). The individual conditional modes occupied a range of correlated tolerance estimates across the spectrum (see Fig. 3), with all age-sex classes having individuals spread across large parts of the spectrum. A small number of individuals (seven adult females, two adult males, and

Table 4. FID model summary. Parameter estimates for the model describing the relationship between FID and the predictor variables.

Population-level effects

	Estimate	**Est. Error**	**l–95% CI**	**U-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	0.67	0.1	0.47	0.87	1.00	13,556	28,565
VODI	−0.04	0.01	−0.07	−0.01	1.00	45,436	45,243
Engaged	0.14	0.02	0.1	0.18	1.00	97,776	46,015
Open (Habitat)	0.12	0.02	0.08	0.16	1.00	91,775	47,949
Ground (Height)	0.12	0.06	0	0.23	1.00	100,351	48,107
Number of neighbors	−0.08	0.01	−0.09	−0.06	1.00	98,909	47,398
Neighbor flee first	0	0.05	−0.09	0.09	1.00	94,500	45,544
External factors within 5 min	0.01	0.04	−0.06	0.08	1.00	94,487	45,998
Unfamiliar observer (AB)	−0.14	0.08	−0.3	0.03	1.00	19,463	30,667
Trial number	−0.02	0.01	−0.04	−0.01	1.00	21,542	34,353
Unfamiliar observer (AB): Trial number	0.02	0.01	0	0.05	1.00	17,996	27,736
Family specific (log-normal)							
Sigma	0.36	0.01	0.34	0.37	1.00	55,469	45,557
Group-level effects							
Date (58 levels)							
sd(Intercept)	0.14	0.02	0.11	0.19	1.00	17,300	31,725
Individual identity (69 levels)							
sd(Intercept)	0.49	0.05	0.4	0.6	1.00	13,780	25,841
sd(VODI)	0.06	0.02	0.02	0.09	1.00	10,338	13,826
sd(ObserverAB)	0.18	0.04	0.1	0.26	1.00	17,276	16,843
sd(TrialNo)	0.01	0	0	0.02	1.00	11,643	13,855
sd(ObserverAB:TrialNo)	0.01	0.01	0	0.02	1.00	8,880	18,037
cor(Intercept,VODI)	0.26	0.22	−0.16	0.7	1.00	22,518	25,743
cor(Intercept,ObserverAB)	0.04	0.2	−0.33	0.44	1.00	34,506	35,920
cor(VODI,ObserverAB)	0.16	0.28	−0.39	0.68	1.00	10,048	18,984
cor(Intercept,TrialNo)	−0.46	0.25	−0.84	0.15	1.00	43,028	29,416
cor(VODI,TrialNo)	−0.25	0.33	−0.81	0.45	1.00	17,519	28,304
cor(ObserverAB,TrialNo)	−0.39	0.29	−0.86	0.26	1.00	21,982	31,250
cor(Intercept,ObserverAB:TrialNo)	−0.12	0.33	−0.73	0.56	1.00	45,303	39,936
cor(VODI,ObserverAB:TrialNo)	−0.36	0.35	−0.88	0.47	1.00	26,569	34,646
cor(ObserverAB,ObserverAB:TrialNo)	−0.05	0.37	−0.7	0.69	1.00	31,439	41,766
cor(TrialNo,ObserverAB:TrialNo)	−0.13	0.39	−0.77	0.67	1.00	19,037	35,675

one juvenile) seem particularly sensitive to approaches by observers (high values on both axes), while two adult females, one adolescent, and six juveniles appear exceptionally tolerant of approaches by observers.

DISCUSSION

Our findings indicate that the behavioral responses of baboons to approaches by human observers were most consistent with responses toward high-ranking social threats (passive displacement), although active responses were also recorded on rare occasions. This suggests that human observers are not neutral to habituated primates. We failed to detect any evidence that a suite of environmental (height), social (neighbor flight and external events), and methodological/observer variables (observer identity and trial number) influenced VOD or FID. Although some factors (such as baboon behavior at that start of approach, habitat, and number of neighbors) played a role in how quickly baboons visually oriented toward

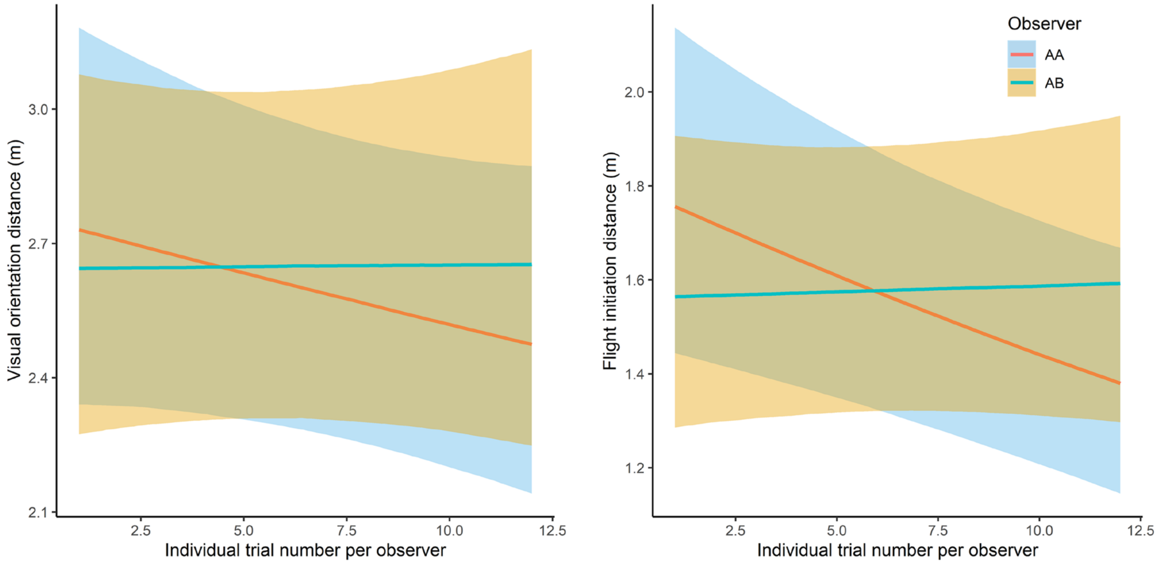

Fig. 2. Conditional effect plots for interaction between observer identity and individual trial number per observer from VOD and FID models. The plot represents conditional predictions of the regression curve when all fixed effects are held constant apart from the interaction (observer × individual trial number per observer); the mean was used as the measure of central tendency, with the shaded areas displaying the relevant credible intervals (2.5 and 97.5% percent quantiles). AA represents the familiar observer, and AB represents the unfamiliar observer.

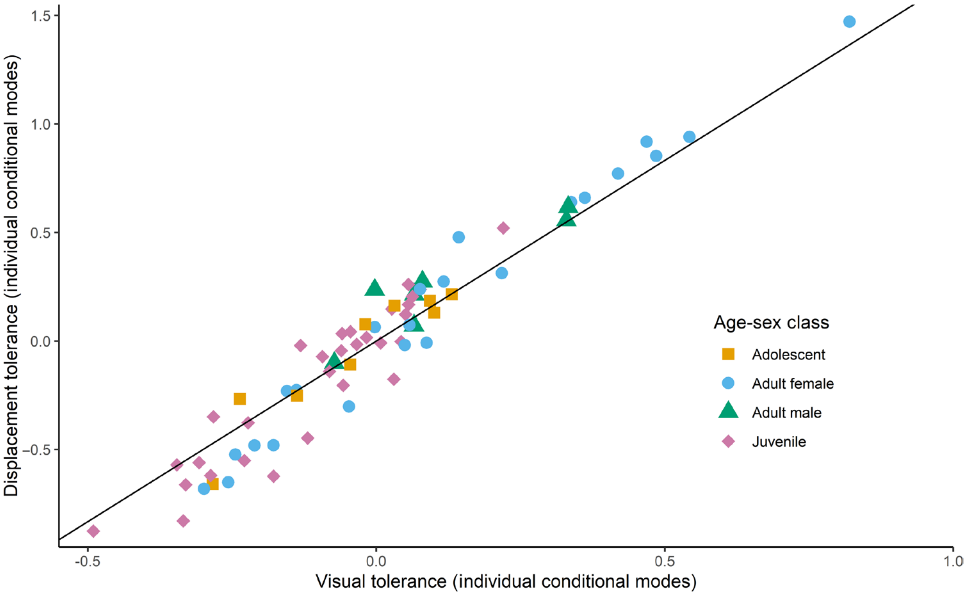

Fig. 3. Convergent validity regression. Regression relationship between visual tolerance and displacement tolerance. Estimates were derived from bivariate Bayesian model; lower values indicate greater "tolerance." Each point represents the conditional modes of an individual baboon ($n = 69$) for each tolerance trait.

or were displaced away from an approaching observer, these factors were largely overshadowed by the role of individual identity in predicting when visual orientation or displacement would occur. Bayesian stacking weights [see (*27*)] strongly favored the models inclusive of individual identity, suggesting that VOD and FID responses were distinct among individuals, providing support for prediction 1: Individual baboon identity should account for a larger degree of the variance in VOD and FID than other variables. In addition, ICC estimates revealed that VOD and FID were consistent within individuals (i.e., repeatability), supporting prediction 2: within-individual consistency in VOD and FID responses. Last, we found a strong correlation between visual and displacement tolerance, supporting prediction 3: VOD and FID are different measures of the same personality trait, i.e., convergent validity. Together, these results suggest that two implicit assumptions concerning habituation in wild animals are not applicable to this group: first, that observers were considered neutral and, second, that habituation (i.e., tolerance) was equal across study animals.

Research into animal personalities has grown expansively, exploring traits such as aggressiveness, shyness/boldness, avoidance of novelty, exploration and activity, and sociality (*18*, *33*). Our study is the first to show empirically that tolerance toward human observers is a personality trait in wild, habituated animals. Focus on individual animals is somewhat lacking in FID literature thus far, with individual repeatability often assumed (*34*). Our approach illustrates that extensive, robust sample sizes can be obtained for animals in the wild and so provide a framework for future research. While these findings could be considered a single-group specific phenomenon, the implications of such a personality trait has important implications for primate behavioral ecology and animal behavior studies in general (as discussed below) and so is in need of further research in other contexts. Our framework for recording the behavioral response of animals as a result of each approach (see Table 2) is relatively simple to design and implement and therefore should be easy for future behavioral studies to incorporate. The approach should also be an important precursor to any FID research, as it is often assumed that humans are considered equivalent to predators (*35*). This assumption was not supported in this study and may become questionable as wild populations become increasingly exposed to anthropogenic disturbance (*36*).

We found an exceptionally strong correlation between individual displacement and visual tolerance traits, a result we interpret as a true biological effect. We did not detect any evidence of a heteroskedastic relationship throughout the convergent validity analyses (see Fig. 3), suggesting that individuals have similar levels of visual and displacement tolerance. To validate this result and control for alternative explanations, we subset our data into two evenly sampled and independent datasets; the VOD dataset used even trial numbers (trial numbers 2, 4, 6, etc.), while the FID dataset used odd trial numbers. We ran the same bivariate Bayesian mixed model, ICC, and convergent validity analyses, with almost identical results (see table S2). There is thus a high degree of confidence in the results and issues relating to the envelope constraint found in typical FID analyses [see (*37*)] that were not driving this correlation, and neither were problems relating to shared method variance [see (*24*)]. As a result, there are clear biological grounds for suggesting convergent validity between these factors.

One criticism of our methodological approach may be that direct approaches toward focal animals do not mimic the intent of observers when collecting behavioral observations on wild animals (i.e., observers are normally attempting to be neutral). Nevertheless, incidental displacements inevitably occur throughout the observation process; whether wild animals detect a difference between "accidental" and "deliberate" approaches is up for debate. Since we found consistent visual orientation and flight responses across a range of start distances (SDs) (range, 2.5 to 33.8 m; table S3), it seems unlikely that "sensitive" individuals in the study group only visually orient toward observers when they consider them to be directly approaching them. One methodological adaption may be to use approaches that move parallel to the focal animal or are designed to pass by the animal at predetermined distances; however, this approach would likely not produce a distance measure for all individuals as tolerant phenotypes may not respond to approaches in any detectable way. Therefore, direct approaches (on habituated animals) are likely required if research is focused on measuring VOD and FID within a personality paradigm. However, specifying a common SD and varying approach angles systematically would be an interesting area for future research to explore. This could be particularly enlightening for understanding other questions, such as how the number of observers concurrently observing habituated animals could influence a group's activity budgets, e.g., increasing the number of observers increases the number of visual stimuli that "intolerant" individuals need to attend to (visual) or avoid (displacement).

Alongside the personality findings, we found that baboons using any form of "looking" behavior appeared able to detect approaching observers quickest; however, the mean conditional effect difference between "engaged" and looking was 57 cm, suggesting that baboons have the sensory capacity to detect local threats regardless of their behavior. This is an interesting result when applied to the typical notions of a foraging-vigilance trade-off found throughout vigilance research on several taxa [e.g., (*38*–*40*)]. Do baboons need to be vigilant to detect threats? Active engagement in foraging or grooming appeared to hinder "detection" at only a very minor level, especially when considering that SDs for approaches covered a broad range of distances (range, 2.5 to 33.8 m). These results suggest that baboons do not need to be "vigilant" for approaching threats to detect them. It could be possible that during engaged behaviors, baboons are able to switch to using auditory cues to monitor the position of approaching threats. The result that VOD decreased (detection time increased) as number of neighbors increased may support this notion, as additional conspecifics may mask the audible cues associated with the approaching observer (see table S1). Although more work is required in this area, our results suggest that baboons may be able to collect multiple types of information concurrently, especially when stimuli are local. This finding is valuable for primate vigilance research, as compatibility between general looking/scanning behaviors and threat detection has proved a popular assumption in many studies to date (*41*).

The assumption that observers play little role in the behaviors that they record is implicit throughout animal behavior research, with habituation assumed to lead to study animals "ignoring" human observers or that observer presence is rarely disruptive [e.g., (*4*, *42*, *43*)]. Our results challenge this assumption, but the methodological and statistical approaches that we used offer future researchers a number of tools for ameliorating these observer-related issues. The framework can be used to produce visual and displacement tolerance estimates (i.e., conditional modes) for each individual animal. These variables, known as best linear unbiased predictors elsewhere [see (*25*)], could be used as predictor covariates when addressing a range of questions relating to observer affects. Researchers exploring questions relating to individual vigilance or looking patterns may need to control or investigate the role of tolerance in the behaviors that they record (*5*). Factors such as spatial cohesion and position could be partially determined by observer-governed phenotypic assortment, e.g., intolerant individuals occupying spatial positions that reduce the likelihood of being in proximity to observers (*44*). This would lead to biased recording of social networks, but the methods here could help identify these constraints. It has been argued that predation risk is not uniform across a group (*45*), and the methods here could be used to explore the interaction between individual-level tolerance traits and the typical spatial cohesion and positional patterns used by group members to avoid predation; do intolerant phenotypes weigh-up the risk of remaining on the periphery of groups with the risk of being in proximity to observers? Conversely, the human shield effect (*46*), where wild animals may perceive reduced risk of predation when human observers are present, may only be realized by animals with highly tolerant phenotypes. These tolerant phenotypes may also be able to exploit the tolerance differential and use observers as social tools to aid in accessing/retaining food patches or avoiding aggression; individual conditional modes would be a powerful asset for testing these effects.

Our analytical frameworks could be used to inform researchers of appropriate observation distances to sample animals from to reduce the chance of recording biased social network information and to minimize the effect that observers have on spatial cohesion and individual positioning with the group. For example, our study suggests that an observer distance of greater than 17 m would likely be required if the goal is to completely eradicate any localized observer effects (max VOD recoding, 16.7 m; max FID, 15.6 m). A distance of 5 m would still promote visual monitoring in approximately 10% of the group, i.e., seven individuals had average VODs of greater than 5 m, suggesting that while distance protocols could ameliorate observer effects in many instances, it is unlikely that observers could collect detailed observational data while maintaining distances unlikely to affect a focal animal and its neighbors. If future research attempts to conduct similar work, we highlight that our sampling effort was far greater than necessary (24 trials across each individual). When testing the even- and odd-numbered trials separately (as described above), we were able to fit models with 12 trials without convergence warnings or divergent transitions. This suggests that sampling efforts of six to eight trials per individual may be adequate and should make this process achievable in most contexts; hence, individual measures can be captured relatively quickly as a baseline before observation work commences.

We hope that this work can reignite a wider debate concerning the methodological and ethical assumptions relating to undertaking behavioral observations on wild animals in situ, not only in wild primates but also in other species, e.g., mongooses (*4*, *43*) and meerkats (*42*) where direct observations of study subjects is regularly used in research. Our results suggest that human observers are not neutral and that tolerance is not equal across the individuals within our group of habituated chacma baboons. It is unknown to what extent similar factors are at play in the host of other systems monitored by behavioral ecologists around the globe, but there is a need to investigate these factors to ensure that we are not systematically biasing results through our methodological choices.

MATERIALS AND METHODS

Ethics

This research was undertaken under ZA/LP/81996 research permit, with ethical approval from the Animal Welfare Ethical Review Board at Durham University.

Study area

FID approaches were conducted in the field at the Lajuma Research Centre, western Soutpansberg Mountains, South Africa (central coordinates 29.44031°S, 23.02217°E) between October 2017 and April 2018. The altitude of this study area varies from 750 m above sea level to 1748 m at the peak of the mountain range (within the study area). The mountainous environment includes a complex mosaic of natural habitat types that belong to the Afromontane mist-belt communities, with natural habitats varying greatly in their structural characteristics (*47*). Although the majority of the land within the study site is classified as a private nature reserve, ecotourism takes place in these areas, while monoculture crop farming and livestock farming take place locally. These farming practices overlap with the core part of the study baboon group's typical home range, with baboons regularly scared away from farm areas by workers clapping, yelling, or throwing stones; however, serious or fatal conflict has never been observed. The habituated study group appeared to differentiate between observers and farm workers, e.g., baboons will alarm in response to worker presence while concurrently allowing close observer proximity.

Study group

The group was habituated circa 2005 and was the focus of intermittent research until the start of this study [see (*47*)]. Since 2014, the group has received consistent observational research in the form of full-day follows 3 to 4 days a week, with occasional gaps of up to a duration of 5 weeks. The group was typically followed from dawn to dusk on a 4 days on–3 days off schedule designed to maintain as much of their natural interactions with predators as possible. The study group contained between 76 and 85 individuals over the course of the study. One confirmed predation of an adult male baboon by an adult male leopard took place, while several other disappearances occurred, although the causes were unconfirmed. A total of 69 individuals were used in the final analyses: 21 adult females, 7 adult males, 4 adolescent males, 7 adolescent females, 13 juvenile females, and 21 juvenile males. Across the study period, several individuals changed age-sex class category (see text S1 for descriptions); as a result, the total number of individuals sampled does not equal the cumulative total for each age-sex class.

FID approach procedure

When a focal animal was encountered, the observer moved to an appropriate distance (based on the distribution of previous approaches) and angle relative to the focal animal. This position had to be within a 90° field of view of the front of the focal animal's head (45° either side of center), i.e., the focal animal's head had to be broadly facing forward. Approaching from outside of this angle may have been challenging for baboons to detect approaching observers visually, forcing focal animals to rely on other cues instead. As baboons can rotate their heads quite far, this was more appropriate than using orientation of the focal animal's body to judge start position. The approaching observer would wait for at least 10 s at the start position before commencing an approach and would only start an approach if there was no obvious response from the focal animal within this time. Trials were abandoned after 30 s if an approach was not started, such as where another baboon sat between observer and focal animal before starting the approach, the focal animal turned its head so that we could no longer approach directly within their visual field, or the focal animal was already looking toward the observer. In all scenarios, another focal animal was selected instead.

When ready to start the approach, we dropped a marker (a blue and purple spray-painted rock approximately 2 cm in diameter) behind our feet (to mark the SD). In all approaches, observers walked directly to the focal animal's start position, without pausing at any point (*19*). During the approach, we dropped additional stones behind our legs to mark VOD, neighbor flight distance (i.e., neighbor within 5 m at start of approach is displaced before focal animal), and FID (i.e., the distance at which the animal moved away from its original position as a result of the approach). VOD was operationally defined as the focal animal directing their line of vision toward the face of the approaching observer, a behavioral marker shown during pilot work to be associated with detection of our approach. There were no instances of additional baboons interrupting the approaches or moving in between the focal animal and the approaching observer; however, approaches would have been abandoned in such circumstances.

Stones consistently landed in accurate locations, but a second observer was always present several meters behind the start position to confirm the location of the stones was accurate or subsequently adjust the position of stones that bounced into inaccurate positions. As each observer dropped the markers behind their legs during the approach, the sound of the small stone landing was apparently either masked by the observer's footsteps (and other local noises) or was not a sufficient stimulus to warrant a visual orientation or flight. We did not observe any focal animal respond to the markers landing; however, approaches would have been abandoned if this had happened. We repeated three approaches when juvenile baboons picked up the stones. Distances between markers and the start position of the focal animal were then measured using a laser range finder (Leica DISTO DXT) and recorded on an electronic device (Samsung Galaxy J5, Samsung Town, Seoul, Republic of Korea), using a personalized application built with the software CyberTracker v3.466 (CyberTracker Conservation, Bellville, South Africa; http://www.cybertracker.org). After the approach was successfully completed, we noted the behavioral response of the focal animal (behaviors listed in Table 2). We excluded the behavioral marker "tail up," as this can be hard to identify because of individual tail use varying.

Sampling design and justification

To produce an equal sampling effort across the study group, each individual study animal was subjected to 12 approaches by two observers (24 in total). One observer was considered familiar (AA, had followed the group for approximately 3 years), and the second observer was considered unfamiliar (AB, conducted first FID approach on the first day with study group); the unfamiliar observer was always in proximity to the familiar observer, which may have diminished the initial novelty/threat perceived by the study group (toward the unfamiliar observer). The presence of the familiar observer was essential, however, to ensure accurate identification of study animals.

To confirm that both observers were making identical judgements for VOD and FID, we undertook 60 pilot trial approaches (30 for each observer). For each approach, one observer would drop the markers for VOD and FID, and the second observer would observe the approach and note whether they agreed with where markers were dropped on the basis of the focal animal's behavioral responses. Both observers were in agreement for all distances throughout pilot work, i.e., the second observer did not disagree with the placement of the stones for either observer for any trial, suggesting a robust definition framework.

To control for time of day, each day was split into four time periods that were adjusted seasonally to ensure that each accounted for 25% of the current day length. We recorded six samples in each time period, three by each observer. Since certain intolerant animals were harder to sample (i.e., would displace before allowing FID approaches), focal individuals were selected pseudorandomly but sampled evenly across each time period. On average, 29 approaches were completed each day (min = 1 and max = 83) across 58 sampling days. We limited each individual to a maximum of two approaches within a single day.

The effect of SD has received a great deal of attention and is one of the strongest and most widely reported effects in FID literature [see (*48*)]. SD is determined by the observer, with recent best practice recommendations suggesting that researchers should systematically vary this distance to get a true understanding of the dynamics of escape behaviors (*19*). We attempted to distribute SDs evenly from close (approximately 3 m) to distant (8 m and beyond) for each individual (see table S3). These distances reflect the normal range of distances used when collecting behavioral data on the study group. Although most individuals received approaches across an even distribution of SDs, certain individuals did not permit close SDs (see table S3).

We controlled for approach speed by using a controlled walking pace during observational data collection. Both observers measured their walking speeds before study (20 trials walking between 5-m markers) and aligned their walking speeds to one another, resulting in almost identical walking speeds when tested again (20 observations each; AA: mean = 0.84 m/s, min = 0.74, and max = 0.95; AB: mean = 0.81 m/s, min = 0.76, and max = 0.90). When approaching, we focused our gaze on the focal animal's forehead to maintain the same speed and posture throughout the approach (*49*). In addition, it allowed both observers to easily identify each parameter (visual orientation, neighbor movement, and flight). Direct eye contact was avoided, as this can startle baboons and is similar to their natural dominance behaviors.

Contextual variables

As baboons can change behavior rapidly, we made no attempt to restrict approaches to certain behaviors; instead, we used an instantaneous scan sampling method to record contextual variables at the instant we commenced an approach. We recorded the following factors (see Table 1): whether the focal animal was performing engaged (foraging, giving grooming, and autogrooming) or non-engaged (resting, receiving grooming, and chewing food) behaviors, looking [see (*41*)] or not looking, whether the animal was on the ground/aboveground, current habitat type (open/closed), number of neighbors within 5 m of the focal animal, and alarms or aggressions within 5 min before approach. During the process, we noted the trial number that each individual baboon had received per observer, i.e., separate trial number scores of 1 to 12 for each observer.

We made approaches in all the habitats that the baboons use (see text S2 for descriptions) but did not undertake approaches where individuals were adjacent to large rocks or cliff edges, as these limit escape options. Approaches were only made when there were no obstructions between the focal baboon and the approaching observer, allowing consistent posture and head and eye direction. We did not systematically vary the habitat that we undertook approaches for each individual; as a result, certain individuals may have received approaches in some habitats more than others. We did make approaches toward individuals sat on small rocks or low-hanging branches within 0.5 m off the ground; this was recorded as a categorical variable (above ground/on ground). We did not attempt approaches on individuals higher than this, as the approach would no longer be direct, as the observer could not directly walk through the target animal's start location. Alarms or aggressions could be from any individual within the group and were simply used as a proxy for increased risk perception. Last, we chose 5 m as the distance for recording number of neighboring conspecifics, as this was a well-practiced measurement consistently undertaken during previous research on this baboon group by AA and reflects a compromise between maximizing information in high-visibility areas and minimizing error in low-visibility habitats.

Statistical analysis

Drivers of VOD and FID

We used complete (i.e., maximal/global) models for both VOD and FID analyses (inclusive of all contextual effects; Table 1). The VOD and FID models included VODD and VODI, respectively, as covariates to control for envelope constraint (see Materials and Methods). The only interaction term included was the interaction of observer identity and trial number, as this explored whether any habituation/sensitization effects took place for each observer through time while investigating the separate effects of observer identity and trial number on both VOD and FID. We fitted both models with random intercepts over date and individual identity. We additionally specified a random slope for the interaction between observer identity and trial number over individual identity, allowing the rate at which individuals habituate/sensitize to each observer to vary between individuals. All varying effects of individual identity were modeled as correlated. The inclusion of individual identity was validated using log-score stacking to combine Bayesian predictive distributions, which is recommended in an "M-open" situation (*27*).

The "compatibility" variable only appeared in the VOD model as, theoretically, the distinction between looking, engaged, and "not looking not engaged" should only influence the VOD response variable. The variable "engaged/not engaged" was only included for FID as a measure of the focal animal having costs associated with early departure, i.e., loss of social time or foraging patch. The variables of habitat (open/closed), number of neighbors, neighbor flight, and aggressions/alarms within 5 min of the start of the approach were considered for both VOD and FID. We did not explore the factors determining why a focal animal may have been looking at the start of an approach, but factors such as number of neighbors and aggressions/alarms within 5 min could alter risk perception and subsequently prime an individual to respond faster to an approaching threat, e.g., increasing neighbors could decrease risk perception, resulting in slower visual orientation and shorter VOD; the opposite would potentially be true for an alarm or aggression within 5 min, i.e., increased risk perception leading to individuals having a faster tendency to visually orient, thus producing a longer VOD. The height variable (ground/above ground) was included within for VOD as "above ground" had a maximum of 50 cm and therefore should not alter risk perception but could allow for earlier detection of threats, i.e., increased VOD.

All models were fit using the brm function from the brms package (*50*) in the R software (*51*). The brm function commands samples to be drawn from the posterior distribution via the package Rstan (*52*), which interfaces with the probabilistic programming language Stan via the C++ toolchain in Rtools (*53*). The brm function implements Hamiltonian Monte Carlo in combination with the No-U-Turn Sampler extension. For each model, we ran six Hamiltonian Markov chains for 15,000 iterations (including 5000 warmup iterations) with adapt delta set to 0.95, to provide algorithms that converge efficiently for multilevel models (*50*). The Gelman-Rubin convergence diagnostic [Rhat (*54*)] was used to assess Markov chain Monte Carlo convergences by comparing the estimated within- and between-chain variances of each factor within the model. All models had Rhat of 1.00 for all factors, suggesting very accurate estimates of the posterior distribution (*50*). Normal priors (mean = 0, standard deviation = 100) were assigned for fixed effects within the brm function; the random effects were assigned default half Student *t* priors (df = 3, mean = 0, standard deviation = 10).

All models were fit with log-normal response distributions (family) and default link functions (*50*). Log-normal was initially decided after visual assessment of the response distribution using Cullen and Frey plots (descdist function) and further assessed using the qqcomp function. We subsequently validated this in all candidate models by checking the residual standard deviation of each model, with Rhat = 1.00 in all cases, indicating accuracy of the response variables with regard to the log-normal response distribution, i.e., the standard deviation of VOD/FID points formed around the log-normal functions was minimal. The random structure of all models included fitting the random structure of observation date crossed with individual identity, which was paramount to our personality and habituation/sensitization hypotheses. All models included the intercept; forcing the SD × FID or SD × VOD regressions through the origin has been subject to debate (*55*); however, as we did not start approaches if focal animals were already looking at us and, therefore, SD > VOD, we assumed that the predicted relationship of SD with FID/VOD changes with increasing SD applied and therefore followed the advice in (*55*) and similar work by other authors [e.g., (*22*)].

In recent literature, the FID ≤ alert distance/VOD ≤ SD relationship has been referred to as a "constrained envelope" and results in some underlying issues with analysis due to extreme heteroscedasticity breaking model analysis assumptions. Although other approaches have been suggested, e.g., quantile regression (*56*) and Phi index (*36*), we elected to control for varying SD indirectly by including one of the other independent distance measures, i.e., to standardize the analysis for variance in SD, we included VODD (as a covariate and as a random slope over individual identity) in all models analyzing VOD and VODI (as a covariate and as a random slope over individual identity) in all models analyzing FID (*57*). This allowed us to retain the covariate predictor variables in the analysis, which would not be possible with the Phi index. Quantile regression was not considered, as individual sample sizes were not above the minimum threshold of 50. We discounted a final option of ignoring the intercept of the relationship [see (*48*)], as this has previously been criticized (*36*).

Tolerance as a personality trait: Visual tolerance and displacement tolerance

We tested the personality hypotheses for prediction 1 (VOD and FID distinct among individuals) by comparing Bayesian stacking weights for each maximal model with and without the individual identity random effect. To achieve this, we firstly estimated the pointwise out-of-sample prediction accuracy from each maximal model (VOD and FID) inclusive and exclusive of the individual identity random effect using leave-one-out cross-validation (LOO) from the "loo" package (*58*). loo uses a Pareto smoothed importance sampling (PSIS) procedure for regularizing importance weights when computing LOO (hereafter termed as PSIS-LOO) (*27*). We found good PSIS approximation reliability by inspecting the estimated shape parameter $\hat{k}$ diagnostic values in the generalized Pareto distribution; for all models, we had no left-out data points for which $\hat{k} > 0.7$ (*27*, *59*). Bayesian stacking was undertaken using the "stacking_weights" function from the loo package. Each maximal model was compared to the same maximal model, excluding individual identity using log-score stacking to combine Bayesian predictive distributions. When comparing two models, if the one model does consistently better than the other model at every pair of data points, then the stacking weight is equal to 1 (*59*). Thus, a stacking weight of 1 signifies that one model has predicted every data point better than the other model and offers substantial predictive power over the other model. Personality research has previously used likelihood ratio tests to test statistical significance of repeatability of linear mixed-effects models with and without identity effects (*23*); however, this Bayesian stacking approach has been strongly recommended within a Bayesian framework and highlights the extent to which individual identity accounts for variance within the maximal models (*27*).

We calculated the ICC, otherwise termed repeatability, to assess personality hypothesis prediction 2 (within-individual consistency in VOD and FID). ICC is typically estimated as the ratio of the variance associated with the individual identity effect divided by the total variance, i.e., sum of individual and residual variances, ($\mathrm{VAR}_{\mathrm{ind}}/\mathrm{VAR}_{\mathrm{ind}} + \mathrm{VAR}_{\mathrm{resid}}$), with ICC informing researchers of the degree of variance explained by individual differences, and thus is a measure of individual consistency (*22*). To achieve this, we extracted the relevant variance components from the maximal VOD and FID (univariate) models using the "VarCorr" function, squaring the estimated standard deviations to produce estimated variance values, and used these values to create two new posterior distributions for VOD and FID separately (*25*). The ICC value calculated for individual identity represents the ratio between (i) the variance explained by drawing from the posterior predictive distribution not conditioned on individual identity or observation date and (ii) the variance explained by posterior predictive distribution conditioned on individual identity (with random slopes for VODD/VODI, and the interaction between observer identity and trial number) crossed with observation date (separately). The calculated ICC values (one for each model, VOD and FID) for individual identity controls for the variance explained by observation date and also by the wider fixed effects structure by drawing from the posterior predictive distribution in each calculation phase, therefore producing values equivalent to enhanced agreement repeatabilities (*28*).

To investigate whether visual tolerance (VOD) correlated with displacement tolerance (FID), i.e., convergent validity (*24*) (prediction 3), we used a bivariate Bayesian mixed-effects model fitted with VOD and FID as response variables. The model was fit with the same fixed effects structure from each response variable's maximal model, log-normal response distributions, and the same priors as described for the univariate model analyses. After fitting this model, we extracted the variance components from the model using the VarCorr function, again squaring the relevant standard deviations to calculate estimated variance values. This allowed us to create a posterior distribution of the among-individual correlation by dividing the corresponding variance between VOD and FID by the product of the square root of their individual trait variances, which standardizes their covariances to a scale from −1 to 1.

R code

Univariate maximal VOD model: brm (VOD ~ VODD + Compatibility + Habitat + Height + Number of neighbors + Nearest neighbor flee first + External events within 5 min + Observer*Trial number + (1|Date) + (1 + VODD + Observer*Trial number|p|ID), data = FID, family = log-normal, prior = prior, chains = 6, iter = 15000, warmup = 5000, control = list(adapt_delta = 0.95)).

Univariate maximal FID model: brm (FID ~ VODI + Engaged + Habitat + Height + Number of neighbors + nearest neighbor flee first + external events within 5 min + Observer*Trial number + (1|Date) + (1+ VODI + Observer*Trial number|p|ID), data = FID, family = log-normal, prior = prior, chains = 6, iter = 15,000, warmup = 5000, control = list(adapt_delta = 0.95)).

Bivariate model:

Mod.VOD ≤ bf (VOD ~ VODD + Compatibility + Habitat + Height + Number of neighbors + Nearest neighbor flee first + External events within 5 min + Observer*Trial number + (1|Date) + (1+ VODD + Observer*Trial number|p|ID) + log-normal().

Mod.FID ≤ bf (FID ~ VODI + Engaged + Habitat + Height + Number of neighbors + nearest neighbor flee first + external events within 5 min + Observer*Trial number + (1|Date) + (1+ VODI + Observer*Trial number|p|ID) + log-normal().

Bivariate.Mod ≤ brm (mod.vod + mod.fid, data = fid, prior = prior, chains = 6, iter = 15,000, warmup = 5000, control = list(adapt_delta = 0.95)).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/28/eaaz0870/DC1

View/request a protocol for this paper from *Bio-protocol*.

REFERENCES AND NOTES

1. D. T. Blumstein, Habituation and sensitization: New thoughts about old ideas. *Anim. Behav.* **120**, 255–262 (2016).
2. P. Bertolani, C. Boesch, Habituation of wild chimpanzees (*Pan troglodytes*) of the South Group at Taï Forest, Côte d'Ivoire: Empirical measure of progress. *Folia Primatol.* **79**, 162–171 (2008).
3. L. M. Fedigan, Ethical issues faced by field primatologists: Asking the relevant questions. *Am. J. Primatol.* **72**, 754–771 (2010).
4. A. le Roux, M. I. Cherry, M. B. Manser, The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Anim. Behav.* **75**, 943–949 (2008).
5. R. J. Welch, A. le Roux, M. B. Petelle, S. Périquet, The influence of environmental and social factors on high- and low-cost vigilance in bat-eared foxes. *Behav. Ecol. Sociobiol.* **72**, 29 (2018).
6. B. M. Titus, M. Daly, D. A. Exton, Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the bay islands, honduras. *PLOS ONE* **10**, e0119645 (2015).
7. B. B. Smuts, *Sex and Friendship in Baboons* (Harvard University Press, 1999).
8. K. T. Hanson, E. P. Riley, Beyond neutrality: The human–primate interface during the habituation process. *Int. J. Primatol.* **39**, 852–877 (2017).
9. L. Alcayna-stevens, Habituating field scientists. *Soc. Stud. Sci.* **46**, 833–853 (2016).
10. M. Candea, Habituating meerkats and redescribing animal behaviour science. *Theory Cult. Soc.* **30**, 105–128 (2013).
11. S. D. Gosling, From mice to men: What can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86 (2001).
12. E. A. Williamson, A. T. C. Feistner, Habituating primates: Process, technique, variables and ethics, in *Field and Laboratory Methods in Primatology: A Practical Guide*, J. M. Setchell, D. J. Curtis, Eds. (Cambridge Univ. Press, ed. 2, 2011), pp. 33–50.
13. K. M. Jack, B. B. Lenz, E. Healan, S. Rudman, V. A. M. Schoof, L. Fedigan, The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am. J. Primatol.* **70**, 490–494 (2008).
14. P. McDougall, Is passive observation of habituated animals truly passive? *J. Ethol.* **30**, 219–223 (2012).
15. S. K. Iredale, C. H. Nevill, C. K. Lutz, The influence of observer presence on baboon (*Papio spp.*) and rhesus macaque (*Macaca mulatta*) behavior. *Appl. Anim. Behav. Sci.* **122**, 53–57 (2010).
16. M. C. Crofoot, T. D. Lambert, R. Kays, M. C. Wikelski, Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Anim. Behav.* **80**, 475–480 (2010).
17. A. J. Carter, H. H. Marshall, R. Heinsohn, G. Cowlishaw, How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Anim. Behav.* **84**, 603–609 (2012).
18. D. Réale, S. M. Reader, D. Sol, P. T. McDougall, N. J. Dingemanse, Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* **82**, 291–318 (2007).
19. D. T. Blumstein, D. S. M. Samia, T. Stankowich, W. E. Cooper, Escaping from predators, *An Integrative View of Escape Decisions*, W. E. Cooper, D. T. Blumstein, Eds. (Cambridge Univ. Press, 2015), pp. 405–419.
20. W. E. Cooper Jr., W. G. Frederick, Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67 (2007).

21. R. C. Ydenberg, L. M. Dill, The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249 (1986).
22. A. J. Carter, R. Heinsohn, A. W. Goldizen, P. A. Biro, Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* **83**, 1051–1058 (2012).
23. M. B. Petelle, D. E. McCoy, V. Alejandro, J. G. A. Martin, D. T. Blumstein, Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**, 1147–1154 (2013).
24. A. J. Carter, W. E. Feeney, H. H. Marshall, G. Cowlishaw, R. Heinsohn, Animal personality: What are behavioural ecologists measuring? *Biol. Rev. Camb. Philos. Soc.* **88**, 465–475 (2013).
25. T. M. Houslay, A. J. Wilson, Avoiding the misuse of BLUP in behavioural ecology. *Behav. Ecol.* **28**, 948–952 (2017).
26. D. T. Blumstein, Flush early and avoid the rush: A general rule of antipredator behavior? *Behav. Ecol.* **21**, 440–442 (2010).
27. Y. Yao, A. Vehtari, D. Simpson, A. Gelman, Using stacking to average bayesian predictive distributions (with Discussion). *Bayesian Anal.* **13**, 917–1007 (2018).
28. M. A. Stoffel, S. Nakagawa, H. Schielzeth, rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639–1644 (2017).
29. T. K. Koo, M. Y. Li, A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163 (2016).
30. J. S. Strong, R. B. Weladji, Ø. Holand, K. H. Røed, M. Nieminen, Personality and fitness consequences of flight initiation distance and mating behavior in subdominant male reindeer (*Rangifer tarandus*). *Ethology* **123**, 484–492 (2017).
31. A. K. Boon, D. Réale, S. Boutin, The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol. Lett.* **10**, 1094–1104 (2007).
32. R. Kliegl, P. Wei, M. Dambacher, M. Yan, X. Zhou, Experimental effects and individual differences in linear mixed models: Estimating the relationship between spatial, object, and attraction effects in visual attention. *Front. Psychol.* **1**, 238 (2011).
33. M. J. Merrick, J. L. Koprowski, Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* **209**, 34–44 (2017).
34. M. Díaz, A. P. Møller, E. Flensted-Jensen, T. Grim, J. D. Ibáñez-Álamo, J. Jokimäki, G. Markó, P. Tryjanowski, The geography of fear: A latitudinal gradient in anti-predator escape distances of birds across Europe. *PLOS ONE* **8**, e64634 (2013).
35. A. Frid, L. M. Dill, Human-caused disturbance stimuli as a form of predation risk. *Ecol. Soc.* **6**, 11 (2002).
36. K. Uchida, K. K. Suzuki, T. Shimamoto, H. Yanagawa, I. Koizumi, Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behav. Ecol.* **30**, 1583–1590 (2019).
37. D. S. M. Samia, D. T. Blumstein, Phi index: A new metric to test the flush early and avoid the rush hypothesis. *PLOS ONE* **9**, e113134 (2014).
38. F.-R. Favreau, A. W. Goldizen, H. Fritz, S. P. Blomberg, E. C. Best, O. Pays, Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos. *Anim. Behav.* **92**, 175–184 (2014).
39. F. Barnier, P. Duncan, H. Fritz, P. Blanchard, D. I. Rubenstein, O. Pays, Between-gender differences in vigilance do not necessarily lead to differences in foraging-vigilance tradeoffs. *Oecologia* **181**, 757–768 (2016).
40. M. Watson, N. J. Aebischer, W. Cresswell, Vigilance and fitness in grey partridges *Perdix perdix*: The effects of group size and foraging-vigilance trade-offs on predation mortality. *J. Anim. Ecol.* **76**, 211–221 (2007).
41. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).
42. T. H. Clutton-Brock, A. Maccoll, P. Chadwick, D. Gaynor, R. Kansky, J. D. Skinner, Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *Afr. J. Ecol.* **37**, 69–80 (2001).
43. N. R. Jordan, F. Mwanguhya, S. Kyabulima, P. Rüedi, M. A. Cant, Scent marking within and between groups of wild banded mongooses. *J. Zool.* **280**, 72–83 (2010).
44. L. Bejder, A. Samuels, H. Whitehead, H. Finn, S. Allen, Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* **395**, 177–185 (2009).
45. G. Roberts, Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086 (1996).
46. K. Nowak, A. Le Roux, S. A. Richards, C. P. J. Scheijen, R. A. Hill, Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* **25**, 1199–1204 (2014).
47. A. L. de Raad, R. A. Hill, Topological spatial representation in wild chacma baboons (*Papio ursinus*). *Anim. Cogn.* **22**, 397–412 (2019).
48. F. Dumont, C. Pasquaretta, D. Réale, G. Bogliani, A. von Hardenberg, Flight initiation distance and starting distance: Biological effect or mathematical artefact? *Ethology* **118**, 1051–1062 (2012).
49. A. M. Runyan, D. T. Blumstein, Do individual differences influence FLIGHT initiation distance? *J. Wildl. Manage.* **68**, 1124–1129 (2004).
50. P.-C. Bürkner, brms : An R package for Bayesian multilevel models using stan. *J. Stat. Softw.* **80**, 1–28 (2017).
51. R Core Team, R: A language and environment for statistical computing, version 3.6.1. *R Found. Stat. Comput* (Vienna, Austria, 2019).
52. Stan Development Team, RStan: The R interface to Stan, *R Found. Stat. Comput.* (Vienna, Austria, 2019).
53. R Core Team, Rtools software, Version 35, *R Found. Stat. Comput.* (Vienna, Austria, 2018).
54. A. Gelman, D. B. Rubin, Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472 (1992).
55. D. S. M. Samia, F. Nomura, D. T. Blumstein, Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* **9**, 20130016 (2013).
56. S. Chamaillé-Jammes, D. T. Blumstein, A case for quantile regression in behavioral ecology: Getting more out of flight initiation distance data. *Behav. Ecol. Sociobiol.* **66**, 985–992 (2012).
57. N. C. Bonnot, A. J. M. Hewison, N. Morellet, J.-M. Gaillard, L. Debeffe, O. Couriot, B. Cargnelutti, Y. Chaval, B. Lourtet, P. Kjellander, C. Vanpé, Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).
58. A. Vehtari, A. Gelman, J. Gabry, Y. Yao, loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models, R Package. version 2.0.0; (2018).
59. A. Vehtari, D. P. Simpson, Y. Yao, A. Gelman, Limitations of "Limitations of bayesian leave-one-out cross-validation for model selection". *Comput. Brain Behav.* **2**, 22–27 (2019).
60. M. Carrete, J. L. Tella, Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**, 167–170 (2010).
61. J. Krause, J.-G. J. Godin, Influence of prey foraging posture on flight behavior and predation risk: Predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264–271 (1996).
62. G. Cowlishaw, Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**, 667–686 (1997).
63. M. J. Camp, J. L. Rachlow, B. A. Woods, T. R. Johnson, L. A. Shipley, When to run and when to hide: The influence of concealment, visibility, and proximity to refugia on perceptions of risk. *Ethology* **118**, 1010–1017 (2012).
64. T. Stankowich, Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* **141**, 2159–2173 (2008).
65. S. L. Lima, Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20 (1995).
66. W. D. Hamilton, Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311 (1971).
67. I. Vine, Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* **30**, 405–422 (1971).
68. A. A. Y. Chan, P. Giraldo-perez, S. Smith, D. T. Blumstein, Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biol. Lett.* **6**, 458–461 (2010).
69. S. L. Lima, Collective detection of predatory attack by birds in the absence of alarm signals. *J. Avian Biol.* **25**, 319–326 (1994).
70. O. Brick, Fighting behaviour, vigilance and predation risk in the cichlid fish Nannacara anomala. *Anim. Behav.* **56**, 309–317 (1998).
71. W. E. Cooper, Variation in escape behavior among individuals of the striped plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *J. Herpetol.* **43**, 495–502 (2009).
72. W. E. Cooper, V. Pérez-Mellado, D. Hawlena, Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards, *Podarcis lilfordi*. *Behav. Ecol.* **17**, 554–559 (2006).
73. P. A. Lagos, A. Meier, L. O. Tolhuysen, R. A. Castro, F. Bozinovic, L. A. Ebensperger, Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Can. J. Zool.* **87**, 1016–1023 (2009S).
74. G. J. Scrimgeour, J. M. Culp, Nordic society Oikos foraging and evading predators: The effect of predator species on a behavioural Trade-off by a Lotic Mayfly. *Oikos.* **69**, 71–79 (1994).
75. T. K. Matson, A. W. Goldizen, D. A. Putland, Factors affecting the vigilance and flight behaviour of impalas. *South African J. Wildl. Res.* **35**, 1–10 (2005).

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Supplementary Materials for

Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait

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Tables S1 to S3
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References

Table S1. Contextual variables that could be major drivers of VOD and FID responses in habituated chacma baboons with examples from literature.

Factors	Link to sensory capacity/FID/personality	Example
Response variable: VOD		
Observer (pseudo-predator) identity, X_1	Unfamiliar observer considered a greater threat, leading to increased risk-perception and tendency to visually orient, resulting in longer VOD	(*9*, *12*)
Trial number, X_2	(i) Increase or decrease in VOD with trial number indicative of habituation or sensitization (respectively) to FID approach methodology (ii) Consistent individual VOD response through time indicates personality trait	(i) (*49*, *60*) (ii) (*22*, *23*)
Compatibility: Not engaged (Looking/Not looking), Engaged (Not Looking) X_3	Looking may enable animals to collect multiple types of information concurrently; in addition, being "not engaged" may afford focal animals a greater sensory capacity for detection. As a result, individuals looking as approach commences will visually orient toward approaching observer sooner resulting in longer VOD; engaged should yield shorter VOD.	(*41*, *61*)
Habitat (open/closed), X_4	(i) "Open" habitats may afford individuals greater visibility increasing likelihood of attending to approaching observer quicker, resulting in longer VOD (ii) Open habitats are generally considered safer for baboons as they permit earlier detection and avoidance of predators, therefore risk perception could be lower, reducing tendency to visual orient towards approaching observer, resulting in shorter VOD (iii) Open habitats may increase risk perception as focal animals are less concealed from potential threats, increasing tendency to visually orient towards approaching observer, resulting in longer VOD. (iv) "Open" habitats have lower refuge availability which may increase risk perception, resulting in longer VOD	(i) (*41*) (ii) (*62*) (iii) (*63*) (iv) (*62–64*)
Height (ground/above ground), X_5	"Above ground" may afford individuals greater visibility, resulting in longer VOD. In this context "above ground" is <50cm from ground level and is unlikely to qualify as potential refuge (see (*62*)) and therefore should not influence risk-perception.	(*41*)
Number of neighbors within 5m, X_6	(i) As number of neighbors increase, the likelihood of a neighbor visually orienting towards the approacher increases, i.e., collective detection, which could result in longer VOD (ii) As number of neighbors increase, the likelihood of predation decreases reducing risk perception and the tendency to visually orient towards the approach observer, resulting in shorter VOD (iii) Increasing number of neighbors may mask both the visual and audible cues associated with the observer's approach, resulting shorter VOD, e.g., neighbors draw visual attention away from observer, or noises from neighbours mask the sounds of observer's footsteps during approach.	(i) Collective detection: (*65*) (ii) Dilution effect: (*66*, *67*) (iii) (*68*)
Neighbor flight, X_7	Local conspecifics initiating flight before the focal animal will increase risk perception and evoke vigilance. Both factors could lead to focal animals visually orienting toward approaching observer sooner, resulting in longer VOD.	Neighbor flight may provide conspecifics information on local threats (*69*)
External factors (local alarms, aggressions within 5 min), X_8	(i) Localized threatening stimuli leads to increased risk perception and tendency to visually orient, resulting in longer VOD (ii) Localized visual and audible stimuli may reallocate some of the focal animal's finite attention, resulting in longer VOD	(i) (*19*) (ii) (*68*)
Response variable: FID		
VODI, X_9	When visual orientation interval (distance between VOD and FID) is long, focal animals will flee sooner, resulting in longer FID.	F.E.A.R hypothesis: (*26*)
Engaged/Not engaged, X_{10}	FID will be higher if focal animal was engaged at the start of the approach, as flight costs are higher because of interrupted social time (i.e., grooming) or loss of food patch (i.e., foraging)	FID lower during agonistic, reproductive or social interactions (*70*, *71*). Animals in higher quality food patches are associated with shorter flight distances (*72–74*).
Observer (pseudo-predator) identity, X_1	Unfamiliar observer is considered a greater threat; therefore, FID should be greater for unfamiliar observer	(*9*, *12*)
Trial number, X_2	(i) Increase or decrease in FID with trial number indicative of sensitization or habituation (respectively) to FID approach methodology (ii) Consistent FID response through time indicates personality trait	(i) (*49*, *60*) (ii) (*22*, *23*)

Habitat (open/closed), X_4	(i) Open habitats are generally considered safer for baboons as they permit earlier detection and avoidance of predators; therefore, risk perception could be lower, resulting in shorter FID (ii) Open habitats may increase risk perception as focal animals are less concealed from potential threats, resulting in longer FID (iii) Open habitats have lower refuge availability which may increase risk perception, resulting in longer FID	(i) (*62*) (ii) (*63*, *64*) (iii) (*62–64*)
Number of neighbors within 5m, X_6	(i) Risk diluted with greater number of neighbors; therefore, FID should decrease as number of neighbors increases. (ii) Increasing number of neighbors increases localised visual and audible stimuli, and therefore may reallocate some of the focal animal's finite attention resulting in decreased FID	(i) Group size effect: (*75*) (ii) (*68*)
Neighbor flight, X_7	Local conspecifics initiating flight before the focal animal will increase risk perception; and therefore, increase FID.	Focal animals may flee sooner based on neighbor flight (*69*)
External factors (local alarms, aggressions within 5 min), X_8	(i) Localized threatening stimuli leads to increased risk perception and therefore increased FID (ii) Localised visual and audible stimuli may reallocate some of the focal animal's finite attention therefore decreasing FID	(i) (*19*) (ii) (*68*)

Table S2. Summary of intra-class correlation and convergent validity validation analyses for independent VOD and FID data points. For both univariate and bivariate models, VOD data was taken from even numbered trials (e.g., trial number 2, 4, 6 etc) and FID data was taken from odd numbered trials, creating independent datasets. Calculations for ICC and convergent validity analyses followed the same protocol as outlined in *Statistical analyses* for the main dataset. Lower and upper HDI refers to highest density intervals for posterior samples at 95% intervals.

Model type	Mean	Lower HDI	Upper HDI
Univariate			
VOD ICC	0.378	0.207	0.546
FID ICC	0.613	0.507	0.717
Bivariate			
VOD ICC	0.345	0.201	0.495
FID ICC	0.591	0.491	0.689
Convergent validity	0.773	0.577	0.94

Table S3. Summary start distances for each individual

ID	Age-sex class	Number of approaches	Min start distance	Max start distance	Average start distance
ARL	J2M	24	2.532	9.587	5.103
ATH	AF	24	3.076	13.161	6.038
BAM	J1M	24	2.941	9.573	4.749
BIX	J2F	24	3.112	9.494	5.471
BLO	AM	24	3.483	9.261	5.351
BOU	AF	24	2.837	10.323	5.105
BOX	AF	24	2.607	9.127	4.973
BRA	AF	24	3.114	10.677	5.271
BRU	AF	24	3.115	9.868	5.220
BUR	J2M	24	3.305	9.687	5.652
CAR	ADF	24	3.289	9.843	5.312
CLO	J1F	24	2.919	8.42	5.165
COR	ADF	24	3.232	9.333	5.639
CRO	ADM	24	3.31	7.571	5.088
DAN	J1F	24	3.087	11.842	5.668
DAV	AM	24	3.412	9.922	5.250
DIC	J1M	24	2.779	9.932	5.411
DIL	J2M	24	2.91	8.466	5.891
DIN	J1M	24	2.817	10.35	5.503
ECH	ADF	24	2.907	8.948	4.696
EGO	AM	24	3.329	11.272	6.162
ELA	AF	24	3.433	13.646	7.909
EVI	AF	24	3.001	10.586	5.883
FLE	AM	24	3.609	10.26	5.675
FUN	J1F	24	2.889	9.993	5.141
GRO	J1M	24	3.026	10.889	5.192
GRU	AF	24	2.937	10.995	5.476
HEA	AF	24	3.14	12.728	6.694
HEN	ADM	24	2.739	10.771	5.442
HUN	J2M	24	3.001	8.138	4.970
JAC	J2M	24	3.075	14.242	5.819
JOS	AM	24	3.37	10.806	6.316
LAR	J1M	24	3.17	10.861	5.632
LAT	J1M	24	3.342	9.447	5.082
LOB	AF	24	2.748	8.693	5.001
LUK	J3M	24	2.73	9.272	5.223
MAN	AF	24	3.504	13.452	6.637
MEL	AF	24	3.239	12.28	7.024
MOU	J1M	24	3.007	8.644	4.869
MUR	ADF	24	3.392	10.478	5.444
NAT	ADM	24	3.507	11.524	5.668
NIC	J1M	24	3.407	11.479	5.933
NOR	AF	24	4.132	12.279	7.237
NOS	AM	24	3.17	17.082	6.589
PIX	AF	24	3.265	9.964	5.853
PON	J1M	24	2.747	9.63	4.897
PRA	J3M	24	2.69	8.85	5.180
PRE	ADM	24	2.98	10.436	5.432
RHO	ADF	24	2.762	8.535	4.909
RIP	AF	24	3.359	10.115	6.453
SAC	J2F	24	2.922	8.404	5.194
SAN	J2F	24	2.751	10.055	5.357
SCA	AF	24	2.946	9.306	5.075
SCO	J1M	24	2.769	9.309	5.040
SEX	AM	24	3.018	11.105	6.885
SIL	AF	24	3.174	33.864	7.243
SLI	AF	24	3.192	10.142	5.570
STE	J1M	24	3.008	8.884	5.465
STI	J1F	24	3.171	9.274	4.950
STR	J2M	24	2.985	9.164	5.596
TER	AF	24	4.262	17.583	8.864
THI	AF	24	3.035	8.541	5.794
TIL	J2F	24	2.989	9.17	5.371
TON	J1F	24	3.407	9.413	5.534
TRI	AF	24	2.581	7.843	4.858
TRU	J1F	24	2.88	11.377	5.179
TUP	AF	24	3.051	8.863	5.724
YOD	J1F	24	3.048	11.576	5.887
YOL	AF	24	4.615	22.162	11.053

Text S1. Age-sex class categories and descriptions

Female baboons:
AF (Adult female) – Attainment of full body size, either cycling regularly, pregnant or lactating. Nipples also enlarge and elongated from suckling infants.
ADF (Adolescent Female) – Nearly adult female size, with the onset of the first sexual swellings. If visible, nipples are much smaller and button-like than that of an adult female.

Male baboons:
AM (Adult male) – All secondary sexual characteristics fully grown, musculature (most noticeably in chest and rump) expands to full adult size.
ADM (Adolescent Male) – Massive growth in secondary sexual characteristics; testes expand, canines and mane grow longer, body size increases to near that of an adult male.
J3M (Juvenile 3 Males Only) – Body size that of an adult female, muzzle further extended to nearly that of an adult male. Testes start to expand and are clearly visible. Mane becomes noticeable.

Juvenile baboons of both sexes:
J2M/F (Juvenile 2) – Little demarcation from previous period, with greater body size. Hair becomes darker, changing to a more adult grey/brown colouration.
J1M/F (Juvenile 1) – Little demarcation from infants, but fully weaned and nutritionally independent. Muzzle starts becoming more elongated and pronounced. Pelage is still lighter than in juvenile 2. Male/female distinction based on genitalia and noticeable absence/presence of a separation in the callosities.

Text S2. Descriptions of the various habitat types categorised in this study

Habitat type – the Lajuma field site and surrounding properties contain a range of habitat types that can be broadly classified into several categories: forest, woodland, bush, camp, farm, marsh, grassland, rock and cliff. These habitat types will vary in their respective structure and therefore influence visibility to a different extent.

“Closed” habitats

Forest: An area composed largely of trees with overlapping crowns forming 60-100% cover. Trees will be mostly tall providing extensive and near continuous shade.
Woodland: Canopy is more open than forest, with 25-60% cover, allowing sunlight to penetrate between the trees. Woodlands may support an understory of shrubs, herbs, or grasses.
Bush: An area where shrubs or are the dominant vegetation. A shrub is a woody perennial plant, smaller than a tree, with several major branches arising near the base of the stem. Areas of extensive tree regeneration, i.e., saplings, can also qualify as bush.

“Open” habitats

Grassland or savannah: Open area covered predominantly with grass. These areas may be devoid of trees entirely but can also contain widely spaced trees with a minimum of 5% cover to a maximum of 25% cover.
Marshland: Exclusively found in flat regions along permanent water streams on peat. Vegetation components of marshlands include reeds, sedges, and grasses.
Rocks: Areas where ground predominantly consists of rocks and boulders, rather than soil.
Road: Dirt roads that run through the study area. Very little traffic (less than 5 vehicles a day) and always at low speeds (less than 10mph). Road use often offers a localised enhancement in visibility for the baboons.
Camp: Used or disused human settlements on Lajuma and neighbouring properties.
Farm: Ottosdal Macadamia farm or area around Ottosdal farmhouse.

REFERENCES AND NOTES

1. D. T. Blumstein, Habituation and sensitization: New thoughts about old ideas. *Anim. Behav.* **120**, 255–262 (2016).

2. P. Bertolani, C. Boesch, Habituation of wild chimpanzees (*Pan troglodytes*) of the South Group at Taï Forest, Côte d'Ivoire: Empirical measure of progress. *Folia Primatol.* **79**, 162–171 (2008).

3. L. M. Fedigan, Ethical issues faced by field primatologists: Asking the relevant questions. *Am. J. Primatol.* **72**, 754–771 (2010).

4. A. le Roux, M. I. Cherry, M. B. Manser, The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Anim. Behav.* **75**, 943–949 (2008).

5. R. J. Welch, A. le Roux, M. B. Petelle, S. Périquet, The influence of environmental and social factors on high- and low-cost vigilance in bat-eared foxes. *Behav. Ecol. Sociobiol.* **72**, 29 (2018).

6. B. M. Titus, M. Daly, D. A. Exton, Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the bay islands, honduras. *PLOS ONE* **10**, e0119645 (2015).

7. B. B. Smuts, *Sex and Friendship in Baboons* (Harvard University Press, 1999).

8. K. T. Hanson, E. P. Riley, Beyond neutrality: The human–primate interface during the habituation process. *Int. J. Primatol.* **39**, 852–877 (2017).

9. L. Alcayna-stevens, Habituating field scientists. *Soc. Stud. Sci.* **46**, 833–853 (2016).

10. M. Candea, Habituating meerkats and redescribing animal behaviour science. *Theory Cult. Soc.* **30**, 105–128 (2013).

11. S. D. Gosling, From mice to men: What can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86 (2001).

12. E. A. Williamson, A. T. C. Feistner, Habituating primates: Process, technique, variables and ethics, in *Field and Laboratory Methods in Primatology: A Practical Guide*, J. M. Setchell, D. J. Curtis, Eds. (Cambridge Univ. Press, ed. 2, 2011), pp. 33–50.

13. K. M. Jack, B. B. Lenz, E. Healan, S. Rudman, V. A. M. Schoof, L. Fedigan, The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am. J. Primatol.* **70**, 490–494 (2008).

14. P. McDougall, Is passive observation of habituated animals truly passive? *J. Ethol.* **30**, 219–223 (2012).

15. S. K. Iredale, C. H. Nevill, C. K. Lutz, The influence of observer presence on baboon (*Papio spp*.) and rhesus macaque (*Macaca mulatta*) behavior. *Appl. Anim. Behav. Sci.* **122**, 53–57 (2010).

16. M. C. Crofoot, T. D. Lambert, R. Kays, M. C. Wikelski, Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Anim. Behav.* **80**, 475–480 (2010).

17. A. J. Carter, H. H. Marshall, R. Heinsohn, G. Cowlishaw, How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Anim. Behav.* **84**, 603–609 (2012).

18. D. Réale, S. M. Reader, D. Sol, P. T. McDougall, N. J. Dingemanse, Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* **82**, 291–318 (2007).

19. D. T. Blumstein, D. S. M. Samia, T. Stankowich, W. E. Cooper, Escaping from predators, *An Integrative View of Escape Decisions*, W. E. Cooper, D. T. Blumstein, Eds. (Cambridge Univ. Press, 2015), pp. 405–419.

20. W. E. Cooper Jr., W. G. Frederick, Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67 (2007).

21. R. C. Ydenberg, L. M. Dill, The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249 (1986).

22. A. J. Carter, R. Heinsohn, A. W. Goldizen, P. A. Biro, Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* **83**, 1051–1058 (2012).

23. M. B. Petelle, D. E. McCoy, V. Alejandro, J. G. A. Martin, D. T. Blumstein, Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**, 1147–1154 (2013).

24. A. J. Carter, W. E. Feeney, H. H. Marshall, G. Cowlishaw, R. Heinsohn, Animal personality: What are behavioural ecologists measuring? *Biol. Rev. Camb. Philos. Soc.* **88**, 465–475 (2013).

25. T. M. Houslay, A. J. Wilson, Avoiding the misuse of BLUP in behavioural ecology. *Behav. Ecol.* **28**, 948–952 (2017).

26. D. T. Blumstein, Flush early and avoid the rush: A general rule of antipredator behavior? *Behav. Ecol.* **21**, 440–442 (2010).

27. Y. Yao, A. Vehtari, D. Simpson, A. Gelman, Using stacking to average bayesian predictive distributions (with Discussion). *Bayesian Anal.* **13**, 917–1007 (2018).

28. M. A. Stoffel, S. Nakagawa, H. Schielzeth, rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639–1644 (2017).

29. T. K. Koo, M. Y. Li, A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155–163 (2016).

30. J. S. Strong, R. B. Weladji, Ø. Holand, K. H. Røed, M. Nieminen, Personality and fitness consequences of flight initiation distance and mating behavior in subdominant male reindeer (*Rangifer tarandus*). *Ethology* **123**, 484–492 (2017).

31. A. K. Boon, D. Réale, S. Boutin, The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol. Lett.* **10**, 1094–1104 (2007).

32. R. Kliegl, P. Wei, M. Dambacher, M. Yan, X. Zhou, Experimental effects and individual differences in linear mixed models: Estimating the relationship between spatial, object, and attraction effects in visual attention. *Front. Psychol.* **1**, 238 (2011).

33. M. J. Merrick, J. L. Koprowski, Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* **209**, 34–44 (2017).

34. M. Díaz, A. P. Møller, E. Flensted-Jensen, T. Grim, J. D. Ibáñez-Álamo, J. Jokimäki, G. Markó, P. Tryjanowski, The geography of fear: A latitudinal gradient in anti-predator escape distances of birds across Europe. *PLOS ONE* **8**, e64634 (2013).

35. A. Frid, L. M. Dill, Human-caused disturbance stimuli as a form of predation risk. *Ecol. Soc.* **6**, 11 (2002).

36. K. Uchida, K. K. Suzuki, T. Shimamoto, H. Yanagawa, I. Koizumi, Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behav. Ecol.* **30**, 1583–1590 (2019).

37. D. S. M. Samia, D. T. Blumstein, Phi index: A new metric to test the flush early and avoid the rush hypothesis. *PLOS ONE* **9**, e113134 (2014).

38. F.-R. Favreau, A. W. Goldizen, H. Fritz, S. P. Blomberg, E. C. Best, O. Pays, Within-population differences in personality and plasticity in the trade-off between vigilance and foraging in kangaroos. *Anim. Behav.* **92**, 175–184 (2014).

39. F. Barnier, P. Duncan, H. Fritz, P. Blanchard, D. I. Rubenstein, O. Pays, Between-gender differences in vigilance do not necessarily lead to differences in foraging-vigilance tradeoffs. *Oecologia* **181**, 757–768 (2016).

40. M. Watson, N. J. Aebischer, W. Cresswell, Vigilance and fitness in grey partridges *Perdix perdix*: The effects of group size and foraging-vigilance trade-offs on predation mortality. *J. Anim. Ecol.* **76**, 211–221 (2007).

41. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).

42. T. H. Clutton-Brock, A. Maccoll, P. Chadwick, D. Gaynor, R. Kansky, J. D. Skinner, Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *Afr. J. Ecol.* **37**, 69–80 (2001).

43. N. R. Jordan, F. Mwanguhya, S. Kyabulima, P. Rüedi, M. A. Cant, Scent marking within and between groups of wild banded mongooses. *J. Zool.* **280**, 72–83 (2010).

44. L. Bejder, A. Samuels, H. Whitehead, H. Finn, S. Allen, Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* **395**, 177–185 (2009).

45. G. Roberts, Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086 (1996).

46. K. Nowak, A. Le Roux, S. A. Richards, C. P. J. Scheijen, R. A. Hill, Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* **25**, 1199–1204 (2014).

47. A. L. de Raad, R. A. Hill, Topological spatial representation in wild chacma baboons (*Papio ursinus*). *Anim. Cogn.* **22**, 397–412 (2019).

48. F. Dumont, C. Pasquaretta, D. Réale, G. Bogliani, A. von Hardenberg, Flight initiation distance and starting distance: Biological effect or mathematical artefact? *Ethology* **118**, 1051–1062 (2012).

49. A. M. Runyan, D. T. Blumstein, Do individual differences influence FLIGHT initiation distance? *J. Wildl. Manage.* **68**, 1124–1129 (2004).

50. P.-C. Bürkner, brms : An R package for Bayesian multilevel models using stan. *J. Stat. Softw.* **80**, 1–28 (2017).

51. R Core Team, R: A language and environment for statistical computing, version 3.6.1. *R Found. Stat. Comput* (Vienna, Austria, 2019).

52. Stan Development Team, RStan: The R interface to Stan, *R Found. Stat. Comput.* (Vienna, Austria, 2019).

53. R Core Team, Rtools software, Version 35, *R Found. Stat. Comput.* (Vienna, Austria, 2018).

54. A. Gelman, D. B. Rubin, Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472 (1992).

55. D. S. M. Samia, F. Nomura, D. T. Blumstein, Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* **9**, 20130016 (2013).

56. S. Chamaillé-Jammes, D. T. Blumstein, A case for quantile regression in behavioral ecology: Getting more out of flight initiation distance data. *Behav. Ecol. Sociobiol.* **66**, 985–992 (2012).

57. N. C. Bonnot, A. J. M. Hewison, N. Morellet, J.-M. Gaillard, L. Debeffe, O. Couriot, B. Cargnelutti, Y. Chaval, B. Lourtet, P. Kjellander, C. Vanpé, Stick or twist: Roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).

58. A. Vehtari, A. Gelman, J. Gabry, Y. Yao, loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models, R Package. version 2.0.0; (2018).

59. A. Vehtari, D. P. Simpson, Y. Yao, A. Gelman, Limitations of "Limitations of bayesian leave-one-out cross-validation for model selection". *Comput. Brain Behav.* **2**, 22–27 (2019).

60. M. Carrete, J. L. Tella, Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**, 167–170 (2010).

61. J. Krause, J.-G. J. Godin, Influence of prey foraging posture on flight behavior and predation risk: Predators take advantage of unwary prey. *Behav. Ecol.* **7**, 264–271 (1996).

62. G. Cowlishaw, Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**, 667–686 (1997).

63. M. J. Camp, J. L. Rachlow, B. A. Woods, T. R. Johnson, L. A. Shipley, When to run and when to hide: The influence of concealment, visibility, and proximity to refugia on perceptions of risk. *Ethology* **118**, 1010–1017 (2012).

64. T. Stankowich, Ungulate flight responses to human disturbance: A review and meta-analysis. *Biol. Conserv.* **141**, 2159–2173 (2008).

65. S. L. Lima, Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20 (1995).

66. W. D. Hamilton, Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311 (1971).

67. I. Vine, Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* **30**, 405–422 (1971).

68. A. A. Y. Chan, P. Giraldo-perez, S. Smith, D. T. Blumstein, Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biol. Lett.* **6**, 458–461 (2010).

69. S. L. Lima, Collective detection of predatory attack by birds in the absence of alarm signals. *J. Avian Biol.* **25**, 319–326 (1994).

70. O. Brick, Fighting behaviour, vigilance and predation risk in the cichlid fish Nannacara anomala. *Anim. Behav.* **56**, 309–317 (1998).

71. W. E. Cooper, Variation in escape behavior among individuals of the striped plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *J. Herpetol.* **43**, 495–502

(2009).

72. W. E. Cooper, V. Pérez-Mellado, D. Hawlena, Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards, *Podarcis lilfordi*. *Behav. Ecol.* **17**, 554–559

(2006).

73. P. A. Lagos, A. Meier, L. O. Tolhuysen, R. A. Castro, F. Bozinovic, L. A. Ebensperger, Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Can. J. Zool.* **87**, 1016–1023 (2009S).

74. G. J. Scrimgeour, J. M. Culp, Nordic society Oikos foraging and evading predators: The effect of predator species on a behavioural Trade-off by a Lotic Mayfly. *Oikos.* **69**, 71–79 (1994).

75. T. K. Matson, A. W. Goldizen, D. A. Putland, Factors affecting the vigilance and flight behaviour of impalas. *South African J. Wildl. Res.* **35**, 1–10 (2005).

Chapter 5. Investigating whether habituation/tolerance remain consistent after predation events

Flight and visual orientation distance remained consistent in a single group of habituated chacma baboons after an observed predation by a leopard. Do flight initiation distance methods always measure perceived predation risk?

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AA conceived and coordinated the study, carried out statistical analysis, and drafted the initial manuscript. AB collected all field data, participated in statistical analysis, and critically revised the manuscript. AA and AB designed the study with equal contribution. RH participated in statistical analysis and critically revised the manuscript.

Abstract

Flight initiation distance (FID) procedures are used to assess the risk perception animals have for threats (e.g., natural predators, hunters) but it is unclear whether these assessments remain meaningful if animals have habituated to certain human stimuli (e.g., researchers, tourists). Our previous work showed that habituated baboons displayed individually distinct and consistent responses to human approaches, a tolerance trait, but it is unknown if the trait is resilient to life-threatening scenarios. If it were consistent, it would imply FIDs might measure specific human threat perception only and not generalise to other threats such as predators when animals have experienced habituation processes. We used FID procedures to compare baseline responses to the visual orientation distance, FID, and individual tolerance estimates assessed after a leopard predation on an adult male baboon (group member). All variables were consistent despite the predation event, suggesting tolerance to observers was largely unaffected by the predation and FID procedures are unlikely to be generalisable to other threats when habituation has occurred. FID approaches could be an important tool for assessing how humans influence animal behaviour across a range of contexts, but careful planning is required to understand the type of stimuli presented.

Introduction

Flight, fleeing, and escape responses are widely reported anti-predator defences which can directly reduce the chance of an individual being successfully captured (1–5). Optimal escape theory predicts that the distance at which prey decide to flee from an approaching predator, otherwise known as flight initiation distance (hereafter FID), is governed by a trade-off between the risk of being predated upon and the benefits of staying to engage in any fitness enhancing activity (6–9). Therefore, increasing risk of predation should correlate with increased FID (7, 10). Measuring a true FID (in response to an actual predator) is unlikely, and so studies concerning FID and escape behaviour have commonly used approaching researchers to measure FID instead (6, 11–13). This is considered valid in most species and scenarios as humans are often considered predators by these animals (14).

Using human approaches as a surrogate for a predator may be most applicable in areas where humans exert hunting pressure on prey species (e.g., (15, 16)), although elevated FIDs would also be expected where humans are antagonistic towards animals such as in areas of human-wildlife conflict. However, in these elevated anthropogenic risk scenarios it is unclear whether FID measures are exclusively measuring human risk perception, or are generalisable to other threats and particularly predators. Using human approaches to measure perceived predation risk appears less justified in areas where interactions with humans are benign, as animals are known to exhibit lower FIDs as a result of habituation processes (8, 17). Reduced FIDs with increasing anthropogenic disturbance have been reported in several birds species (11, 18–22) and similar effects have been reported in blue-tailed skinks (*Emoia impar*) (23), fox squirrels (*Sciurus niger*) (24), yellow-bellied marmots (*Marmota flaviventris*) (25) and mule deer (*Odocoileus hemionus*) (26). The lower FIDs in these studies suggests diminished risk perception in these animals but FID measures are still considered to reflect the predictions of economic escape theory (8).

If the reduced FIDs found in areas with higher anthropogenic disturbance are indeed still reflective of an animal’s perception of predation risk, then it would suggest that habituation to anthropogenic disturbances can transfer to predators. However, transfer of habituation from humans to predators appears to have only been reported in one instance where urban fox squirrels displayed reduced FIDs in response to human approaches whilst concurrently exhibiting reduced responses to experimental predator stimuli (24); however, the study design has been criticized (see (27)). In the case of (24) it could also be argued that increasing anthropogenic disturbance is associated with reduced predator abundance, which offers a selective advantage to tolerant prey animals (28); as such, the reduction in antipredator behaviours may reflect an absence of experience with predators as opposed to habituation transfer (27). It therefore remains largely unexplored whether diminished risk perception (when quantified by FIDs) is tied specifically to humans. This poses an important question: Do FIDs measure a perception of specific human-risks, or do they reflect the risk perception towards other animals (e.g., predators) or risks more generally?

Recently we explored the visual orientation distance (VOD – the distance at which approached individuals direct their line of vision towards the approaching observer’s face) and FID responses of habituated chacma baboons (*Papio ursinus griseipes*) to approaches from observers and found that individuals displayed consistent VODs and FIDs across repeated approaches that were also highly distinct from one another, allowing individual tolerance estimates to be derived (29). In addition, the habituated baboons viewed observers as equivalent to a high-level social threat despite a long history of observations. Here, we build on these analyses and use a naturally occurring predation event by a leopard (*Panthera pardus*) on an adult male baboon from the study group to assess whether habituated animals alter their risk perception of observers after encountering natural predators. If the predation event had little effect on VOD and FID measures or individual tolerance estimates (of the surviving group members) it would indicate that despite observers being considered equivalent to a high-level social threat, this threat perception is not altered as a result of the predation. If this prediction is met, it would suggest FID methodology is a robust measure of specific human (i.e., researcher) threat perception only when animals have been habituated, and not generalisable to other threats, which would have implications for research exploring antipredator behaviours using FID methodology in scenarios where habituation processes have taken place.

Methods

This research was undertaken under ZA/LP/81996 research permit, with ethical approval from the Animal Welfare Ethical Review Board (AWERB) at Durham University. All data was collected between October and December 2017 on a wild habituated group of Afro-montane chacma baboons (*Papio ursinus griseipes*) in the western Soutpansberg Mountains, South Africa (central coordinates S29.44031°, E23.02217°). For a detailed study site and group description see (29).

The study group was habituated circa 2005 and was the focus of intermittent research attention until 2014. The study area has experienced long-term anthropogenic activities (local farming, forestry, and residences) prior to 2005, and so consistent interactions with humans have been ongoing with this population for some time. Since the initial habituation process was completed several researchers have been able to collect expansive datasets on the study group (e.g., (30, 31)). From 2014 the group received full day (dawn until dusk) follows 3 to 4 days a week, with occasional gaps of up to 5 weeks in duration. The follow schedule was designed to ensure that the study group retained as much of their natural interactions with predators as possible.

The study site was located in a private nature reserve with the majority of the study group's home-range typically overlapping with the core area of the Lajuma Research Centre which contained numerous camps and residences. Interactions with people living in the area, unfamiliar researchers, and tourists were thus a frequent occurrence. However, the baboons had not engaged in 'raiding' residences, threatening humans, or any other potentially negative symptom of habituation prior to the end of this study. The study group were occasionally scared away (chasing, yelling, throwing stones etc) from a small plantation by local workers, usually resulting in fleeing responses and sometimes alarm calling. However, the study group appeared adept at recognising the differences between researchers and these threats. The study group was not hunted during any observation gaps. During this study, the group contained between 81 and 86 individuals.

Non-predation VOD and FID data

All non-predation data was taken from our previous study ((29)). To produce an equal sampling effort across the study group, each non-infant individual (n=69) was originally subjected to 12 approaches by each observer (24 in total) varying in familiarity to the study animals. One observer was considered familiar (AA, had followed the group for approximately 3 years), and the second observer was considered unfamiliar (AB, conducted first FID approach on the first day with study group). For this analysis, data generated by AA was excluded, thus all non-predation and post-predation approaches were completed solely by the unfamiliar observer, AB. Due to time constraints, only a subset of 16 individuals could be sampled repeatedly (3 trials each) post-predation; as such, we only utilised data from the same 16 individuals for our non-predation data. These non-predation trials were used as a baseline for comparison to explore whether the predation event could alter the baboon's typical VOD and FID responses, and ultimately tolerance to observers.

Predation event

Baboons form a significant component of leopard diets in the study region (32, 33). Group-wide alarm calls spread across the study group on November 2nd 2017 at 11:09. Shortly after we discovered the body of an adult male baboon (group member) that had been predated by a leopard on the periphery of the group. The predation event was not directly observed, but inspection of the body indicated the baboon had received a kill bite to the nape of the neck. The baboon was completely motionless by the time of our arrival (approximately half the group was already there), and within minutes the remaining group members (86 at the time) had grouped around the dead baboon. Most group members inspected the body before moving away and looking towards a bush that the leopard may have retreated into. By 11:42 the group had begun dispersing and reengaging in foraging behaviours, except for two adult males who remained with the body. We marked the end of the alarm state in the group as ending at 11:48. At approximately 12:14 the remaining males had re-joined the rest of the group and all individuals continued foraging and moving through a typical part of their range for the afternoon. Camera traps set around the body confirmed the leopard returned a couple of hours later to drag the baboon away.

Post-predation study design

At 11:58 we began a series FID approach trials on a subset of 16 individual group members that evenly represented a number of age-sex classes (6 adult females, 2 adolescent females, 2 juveniles females, 1 adult male, 1 adolescent male, 4 juvenile males). Age-sex class ratios were briefly approximated after the predation event, and focal animals selected from these age-sex classes pseudo-randomly. All individuals were assigned random numbers in an excel spreadsheet (mobile device) and the individuals with the highest values for each age-sex class selected from the list. Individuals retained their random numbers and the first individual in the top five on the list was approached when encountered. Once a trial was completed, this animal was assigned a new random number and reintegrated at the end of the list. As such, some individuals received their 2nd and 3rd trials before others had received their 1st and 2nd trials respectively. Each individual was approached 3 times during the remainder of the day (48 total trials). These post-predation approaches were unique to this study and not used in the previous analysis. The first trial was completed 10 mins after the alarm state had ended, the last trial was 367 minutes after the alarm had ended, whilst the average time since the alarm ended was 186 minutes.

FID approach procedures

The effect of start distance on FIDs has received a great deal of attention in FID research and is one of the strongest and most consistently reported effects (34). It has been recommended that the start distance chosen by observers be systematically varied to achieve a true understanding of the dynamics of flight responses (35). As such, we attempted to distribute our start distances evenly from close (approximately 3 meters) to distant (8 meters and beyond) for each individual. This range of distances was chosen as they reflected typical observation distances. Most individuals received an even distribution of approach distances for non-predation data (29); however, certain intolerant individuals did not permit close start distances. For post-predation data some individuals did not receive a wide distribution of start distances (see dataset) due to the lower number of trials and time constraints limiting the opportunities to complete longer approaches on all subjects, i.e., the further the intended start distance the more likely obstructions and other baboons would be between the observer and the focal. As such, it was more challenging to complete these approaches.

When a focal animal was encountered in a stationary behaviour, the observer selected a start position for the approach according to the focal animal's prior distribution of start distances. This start position had to be within a 90° field of view of the front of the focal animal's head (45° either side of centre), i.e., the animal's face had to be broadly facing forward towards the start position. If approaches were completed outside of the animal's likely field of vision, then it would be challenging for the animal to detect the observers visually, forcing them to rely on other stimuli for detection. Before commencing each approach, the observer waited for at least 10 seconds at the start position before beginning an approach and would only commence if there was no response from the focal animal to our presence within this time frame. We abandoned a trial if another baboon sat between the observer and the focal animal prior to the start of the approach, or if the focal animal turned their head such that we could no longer approach within their field of vision, or the focal was already looking towards either of the observers. Whenever an approach was aborted, another focal animal was selected instead.

We did not vary approach speed systematically and instead attempted to achieve consistent walking pace across all approaches as this mimicked typical observer behaviour whilst observing the study animals. When approaching focal animals the observer was required to focus their gaze on the animal's forehead to maintain the same speed and posture throughout the approach (36), avoid tripping and falling, and to allow the observer to easily identify each behavioural assessment (i.e., visual orientation, neighbour movement, and flight). Direct eye contact was avoided as this can startle baboons and may mimic their typical dominance behaviours. We did not attempt any approaches when the animals were close to large obstructions (e.g., building, rocks, large trees) or cliff edges, as these limit flight options. We made no approaches if there were obstructions between the observer and the focal animal to ensure posture and approach speed remained constant and to ensure the animal was not alerted prematurely by the sound of observers brushing past vegetation or obstructions.

When ready to start an approach, the observer dropped a small painted stone (approx. 2cm in diameter) behind their feet to mark the start distance and dropped further stones to measure VOD and FID. VOD was defined as the focal animal directing their line of vision towards the face of the approaching observer, whilst FID required the animal to move away from its original position as a direct result of the approach. In all approaches the observer walked directly to the focal animal's start position without pausing at any point. In order for an FID observation to be valid it required the animal to visually orient towards the observer before displacing, otherwise it would have been unclear if the animal's movement was a direct response to the approach; however, we had no trials where displacement was not proceeded by visual orientation. We also had no instances of non-focal animals crossing our path as we made our approaches, but approaches would have been abandoned in these situations.

A second observer (AA) was always present further away than the approaching observer to ensure stones landed in accurate locations and to assess the range of contextual variables. We observed no reactions to stones landing on the ground, this was either because the observer's footsteps masked the noise of stones hitting the ground, or the sound was an insufficient stimulus to warrant visual orientation or displacement in any trial; however, if we had observed this, we would have abandoned the trial. Distances between markers and the start position of the focal animal were then measured using a calibrated laser range finder (Leica DISTO DXT) and recorded on an electronic device (Samsung Galaxy J5, Samsung Town, Seoul, Republic of Korea), using a personalized application built with the software CyberTracker v3.466 (CyberTracker Conservation, Bellville, South Africa; http://www.cybertracker.org). After the approach was successfully completed, we noted the behavioural response of the focal animal (behaviours listed in (29)).

Contextual variables

Baboons are able to change between a range of behaviours rapidly, therefore, we elected not to restrict approaches to certain behaviours. Instead, we used an instantaneous point sampling method to record behavioural, social, and environmental variables at the instant we commenced an approach. We recorded the following factors: if the animal was performing engaged (foraging, auto-grooming, and giving grooming) or non-engaged (resting, chewing, receiving grooming) behaviours, looking or not looking, habitat type (open/closed), and number of neighbours within 5 meters. We chose 5 meters as the proximity buffer for recording the number of neighbouring conspecifics as this was a frequently used measurement in other research conducted by AA (which had been validated previously) and reflected a compromise between collecting the most amount of information in high-visibility locations and minimising sampling issues in low-visibility locations. Habitat descriptions are detailed in (29) but briefly, closed habitats were forest, woodland, or bushland habitats characterised by dense woody vegetation, whilst open habitats were largely devoid of similar obstructions and had much higher visibility, including grassland, roads, trails, camps, and rocky areas.

Looking was defined as the focal animals' eyes being open and their line of vision extending beyond their hands and the substrate, animal, or object their hands were in contact with (see (37, 38) for discussion). The premise of this definition is to ensure as much information about the baboons general looking behaviours are recorded, assuming that multiple information acquisition pathways are compatible. For example, an individual looking towards a distant group member likely has more chance of detecting an approaching threat than an individual engaged in a complex foraging task. Our previous results supported that individuals looking at the initiation of our approaches visually oriented the quickest, and individuals not looking due to being engaged in other tasks (e.g., foraging or grooming) had typically longer VODs (29). We also noted the trial number the animal had received so far in the study and during the observation day. Approaches were made across the full range of habitats the study group utilised (see (29) for descriptions), we did not manage to sample each individual evenly across each habitat type.

Statistical analysis

We broke the analysis into two separate approaches. Firstly, we analysed non predation data (n=192 trials) and post-predation data (n=48 trials) separately. In the second approach we combined all observations into a single dataset. In each approach we created separate models for each response variable - visual orientation distance (VOD) and flight initiation distance (FID) - leading to 3 models for each variable (and six total): non-predation data, post-predation data, and combined data. We used Bayesian mixed model analysis to explore a number of potential factors that could influence the VOD and FID of individual baboons. The most-informative predictors of (29) were used in all models; engaged/not engaged behaviours were used only in FID models, whilst compatibility (i.e., engaged, not engaged not looking, or looking) was only used in VOD models. Habitat type and number of neighbours were included in all models. We did not use animal height from our previous study as 'above ground' was not well observed in post-predation trials. Observer identity was not used as trials were only completed by one observer (AB) in this study. The variables of external encounters, neighbour flee first were also removed as they previously offered little predictive power (see (29)) and we did not want to overparameterize models on smaller datasets.

Time period was included as a covariate in all models as post-predation data occurred during the afternoon, and VOD and FID could vary across the day. Time periods were seasonally adjusted to reflect 25% of current day length, all non-predation data was sampled evenly within each time-period at an individual level. For models utilising the non-predation data, individual trial number was included as a numeric variable (as described in (29)). We did not include any variables for time since predation or group trial number post predation as these both accumulated across the group after the event and would therefore be challenging to incorporate into a design focusing on changes at the individual-level. Instead, trial number post-predation was included as a factor variable so that the mean conditional effects of each wave of trials could be easily visualised and compared to the mean conditional effects produced across the 12 non-predation trials. Both VOD and FID were shown to be consistent across the 12 trials for this observer in our previous study, therefore modelling trial number as a factor variable in the post-predation data allowed insights into whether each wave of trials differed from the baseline conditional effects of our previous study. In non-predation and post-predation models trial number was also included as a random slope over individual identity to allow the rate at which individuals habituated/sensitized to the approach stimulus to vary between individuals.

Models utilising the combined non-predation and post-predation dataset were the same except we also included trial type (non-predation or post-predation) as a population-level effect and as a random slope over individual identity, thus allowing the individual responses to the predation stimulus to be modelled. Using total individual trial number (1-12 for non-predation data, 1-3 for post-predation data) would have led to misleading results, as such we instead included individual trial number per day as a population-level effect and as random slope over individual identity for both models using the combined datasets. Date was also included as a group-level factor as each individual (n = 16) was also sampled in the morning prior to the predation event, allowing us to control for any variance that could be explained by observation date.

For all VOD models we included the difference between the start distance and VOD (visual orientation distance delay) as a fixed effect and a random slope, whilst FID models included the difference between VOD and FID (visual orientation distance interval) as a fixed effect and a random slope; in both cases the random slope varied over individual identity. This is a recommended approach to control for the constrained envelope issues found in typical FID analyses as both variable are independent of start distance (29, 39)**.**

All models were fit using the brms package (40). For models using non-predation data and the combined datasets a lognormal response distribution was defined, whilst a Gamma distribution was defined with log link functions for post-predation models. Both distributions are ideal as our dependent variables were distances (i.e., continuous and always positive) and positively skewed, however we assessed the appropriateness of this choice using Cullen and Frey plots (descdist function) and applied posterior predictive checks via visualisation in brms (40). In the case of the post-predation data, we found the Gamma distribution to be a slightly better fit than the lognormal distribution used for the other models.

In all cases default Student t priors (df = 3, Mean = 0, Scale factor = 10) were assigned to all parameters in the brms models. In our previous study we used uninformative flat priors (mean=0, standard deviation=100) as we did not have prior knowledge about our hypothesized predictors' effect on VOD or FID. However, given our previous results we knew most effects were unlikely to be substantially far from zero, thus we decided to use the default 'weakly informative' priors set within brms. Weakly informative priors are able to regularise parameter estimates, whilst parameter shrinkage is greater when statistical power is low, both of which aid confidence in estimates derived from smaller, potentially noisy datasets (41–43). Gelman et al (41) recommended using Student-t priors with a single degree of freedom and a scale factor of 2.5 and 10 for model coefficients and intercepts respectively; however, as mixing is suboptimal for heavy tailed posteriors (as with Student-t with df=1) increasing df above 1 is generally recommended (44). Brms by default utilises a scale factor of 10 for all model intercepts, coefficients, and variance components, we did not alter this as a scale factor of 10 ensured these components could take on a wide range of values. It should also be noted that these parameters are restricted to be non-negative on the standard deviations of the group-level effects, thus a half Student-t prior was implemented for these parameters. We used visualisation of the values of the posterior predictive distribution to confirm our model produced accurate and stable estimates that were not biased by our choice of priors. This was achieved using the pp_check function (brms and bayesplot packages) which compares the observed data to data simulated from the posterior predictive distribution of our models, and in all cases the models produced values similar to our observed data (40, 45).

Non-predation models were run for four Hamiltonian Markov chains for 10000 iterations, both set higher than default settings to aid fitting a relatively small sample size and allowing algorithms to converge efficiently (40). Warmup iterations were set to 4000 and adapt_delta to 0.9, both greater than default to aid in producing robust posterior samples from smaller datasets (40, 46). For combination models and post-predation models the number of chains was increased to 6, warmup was increased to 6000, and adapt_delta to 0.95 for combination models and 0.999 for post-predation models. The Gelman-Rubin convergence diagnostic (Rhat) was equal to 1.00 in all cases suggesting the standard deviation of points formed around the lognormal and gamma functions were minimal. We extracted the conditional modes (known as best linear unbiased predictors elsewhere (e.g., (47)) of each individual baboon from each non-predation and post-predation model, yielding individual visual and displacement tolerance estimates (29) for non- and post-predation data.

Results

VOD was consistent through successive trials in the non-predation dataset (fig 1). Although there was a slight increase in VOD (quicker detection) for trial number 1 after the predation event, the mean conditional effect for trails 2 and 3 post-predation fell within the upper and lower 95% credible intervals for the non-predation data. While VOD was consistent through time periods 3 and 4 after the predation event (see fig S1), the mean conditional effect for time period 4 post-predation was marginally higher than the upper credible interval for time period 4 in the non-predation data. Full summary results for each model are shown in tables S1 and S2.

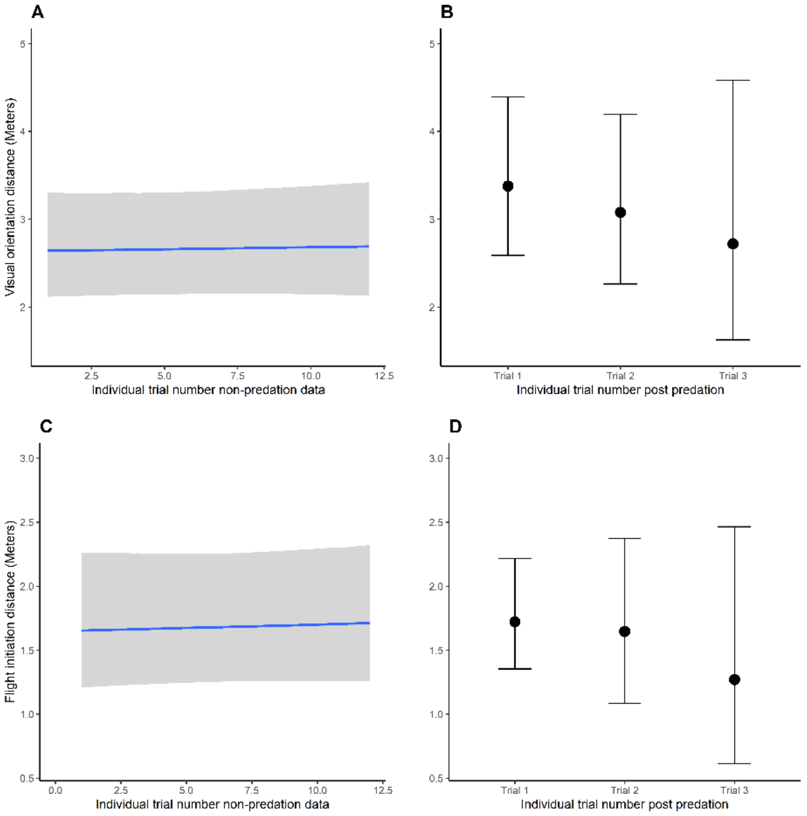

Fig 1. Mean conditional effects for visual orientation distance and flight initiation distance: (a) the relationship between VOD and trial number for non-predation data; (b) the mean conditional effect of VOD for each trial after the predation event; (c) the relationship between FID and trial number for non-predation data; (d) the mean conditional effect of FID for each trial number after the predation event. The shaded areas in (a) and (c) and the tails in (b) and (d) display the relevant credible intervals (2.5 and 97.5 percent quantiles).

FID was consistent through successive trials in the non-predation dataset (fig 1), with a mean conditional effect of 1.68 (1.25,2.27). The mean conditional effect post predation was very similar: trial 1 was 1.72 (1.35,2.22), trial 2 was 1.65 (1.08,2.37), and trial 3 was 1.27 (0.61,2.46). Although the mean conditional effect for trial number 3 was slightly lower, the mean fell within the credible intervals of the non-predation trials. FID was also consistent through time periods 3 and 4 after the predation event (see fig S2), with the conditional means of both time periods for post-predation models falling within the credible intervals of the respective time periods in the non-predation models. Full summary results for each model are shown in tables S3 and S4.

When the non-predation and post-predation datasets were combined, we also found no evidence that VOD or FID were influenced by the predation at the population-level, with both estimates close to zero and 95% credible intervals (C.I) overlapping zero for the post-predation dataset (see trial type (Post predation): tables 1 and 2). For both response variables the results produced for engaged, compatibility, habitat, and number of neighbours matched the findings previously reported in (29).

Table 1. VOD parameter estimates for the model describing the relationship between VOD and the predictor variables. CI, credible interval.

Population-Level Effects:	**Estimate**	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	1.2	0.12	0.96	1.43	1.00	9567	14205
Visual orientation distance delay (VODD)	-0.06	0.03	-0.13	0	1.00	10359	13976
Compatibility (Looking)	0.08	0.05	-0.01	0.17	1.00	19554	19133
Compatibility (Not looking not engaged)	0.03	0.07	-0.1	0.16	1.00	20977	18109
Habitat (Open)	0.18	0.05	0.09	0.27	1.00	14758	16825
Number of neighbours in 5m	-0.05	0.02	-0.08	-0.02	1.00	19391	18317
Time period (2)	0.01	0.06	-0.11	0.12	1.00	17354	18025
Time period (3)	0.11	0.06	-0.01	0.23	1.00	13888	17649
Time period (4)	-0.01	0.07	-0.15	0.12	1.00	11829	16319
Trial type (Post predation)	0.04	0.12	-0.19	0.27	1.00	16567	16600
Individual trial number per day	-0.02	0.05	-0.11	0.07	1.00	14857	15683
Family Specific Parameters:							
sigma	0.25	0.02	0.23	0.29	1.00	8207	14761
Group-Level Effects:							
Date (28 levels)							
sd(Intercept)	0.18	0.05	0.09	0.29	1.00	4503	5289
Individual identity (16 levels)							
sd(Intercept)	0.32	0.09	0.18	0.52	1.00	9409	14780
sd(VODD)	0.09	0.03	0.03	0.17	1.00	5390	5741
sd(Trial type - post predation)	0.15	0.1	0.01	0.39	1.00	5071	9225
sd(TrialNoDay)	0.07	0.04	0	0.17	1.00	4190	7037
cor(Intercept,VODD)	0.02	0.33	-0.57	0.68	1.00	7770	11535
cor(Intercept,Trial type - post predation)	0.09	0.39	-0.69	0.79	1.00	18206	16304
cor(VODD,Trial type - post predation)	0.07	0.42	-0.75	0.81	1.00	13657	16506
cor(Intercept,TrialNoDay)	-0.1	0.39	-0.78	0.69	1.00	14104	15409
cor(VODD,TrialNoDay)	-0.24	0.4	-0.88	0.62	1.00	11742	14945
cor(Trial type - post predation,TrialNoDay)	-0.25	0.45	-0.91	0.7	1.00	7445	14404

Table 2. FID parameter estimates for the model describing the relationship between VOD and the predictor variables. CI, credible interval.

Population-Level Effects:	**Estimate**	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	0.75	0.16	0.44	1.08	1.00	6985	11382
Visual orientation distance index (VODI)	-0.1	0.04	-0.18	-0.01	1.00	19771	16016
Engaged (Not engaged)	0.12	0.05	0.02	0.22	1.00	26547	18721
Habitat (Open)	0.15	0.06	0.03	0.26	1.00	19000	18600
Number of neighbours in 5m	-0.07	0.02	-0.11	-0.03	1.00	26317	18039
Time period (2)	0.01	0.07	-0.13	0.16	1.00	22979	18986
Time period (3)	0.13	0.08	-0.02	0.28	1.00	18205	18364
Time period (4)	-0.03	0.08	-0.19	0.13	1.00	18361	18773
Trial type (Post predation)	0.14	0.15	-0.16	0.43	1.00	16137	16164
Individual trial number per day	-0.05	0.06	-0.16	0.06	1.00	19150	17507
Family Specific Parameters:							
sigma	0.33	0.02	0.29	0.37	1.00	11566	15544
Group-Level Effects:							
Date (28 levels)							
sd(Intercept)	0.16	0.06	0.06	0.28	1.00	5723	5709
Individual identity (16 levels)							
sd(Intercept)	0.51	0.12	0.33	0.8	1.00	9910	13458
sd(VODI)	0.09	0.05	0.01	0.21	1.00	6022	9580
sd(Trial type - post predation)	0.17	0.12	0.01	0.44	1.00	8606	12271
sd(TrialNoDay)	0.09	0.05	0.01	0.21	1.00	5471	9634
cor(Intercept,VODI)	0.11	0.37	-0.61	0.8	1.00	22550	15825
cor(Intercept, Trial type - post predation)	-0.23	0.4	-0.86	0.63	1.00	22709	16218
cor(VODI, Trial type - post predation)	-0.04	0.44	-0.82	0.79	1.00	19082	18381
cor(Intercept,TrialNoDay)	-0.33	0.36	-0.87	0.53	1.00	18947	15477
cor(VODI,TrialNoDay)	-0.1	0.42	-0.83	0.73	1.00	13522	15406
cor(Trial type - post predation,TrialNoDay)	-0.18	0.45	-0.88	0.73	1.00	9922	16938

The group-level effects highlight that there was no evidence that the slopes varied according to trial type (i.e., cor(Intercept, Trial type - post predation), for example, there wasn't a consistent trend for individuals with typically higher or lower VODs during non-predation trials to produce longer or shorter VODs post-predation. Although a small number of individuals exhibited positive or negative slopes across the non-predation and post-predation datasets (see fig 3), the differences were minimal for most individuals, further supporting that the predation event had little influence on the typical VODs and FIDs of the individuals used in this study.

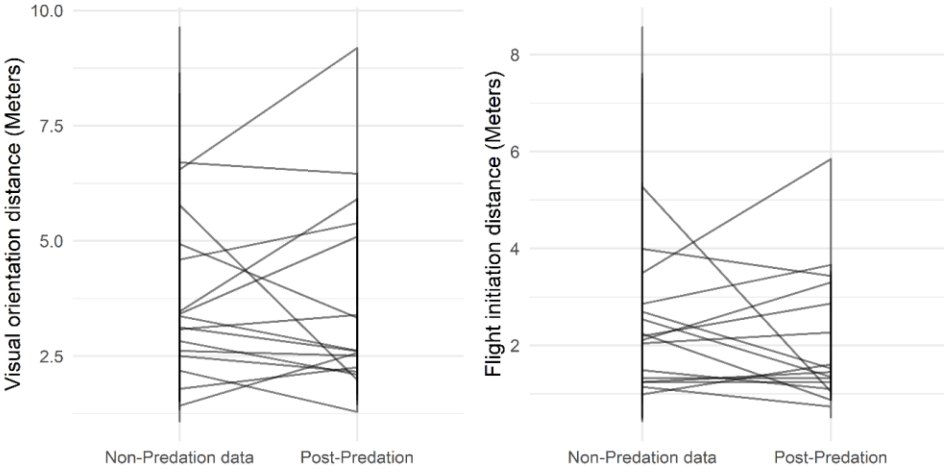

Fig 2. Line graphs representing the predicted individual-level means for VOD and FID for non-predation and post-predation data

Finally, we also found good correlation between individual tolerance estimates (i.e., conditional modes) between non-predation data and post-predation data (fig 3; visual tolerance correlation: (r(14) = .76, p = 0.001); displacement tolerance correlation: (r(14) = .703, p = 0.002)), highlighting that tolerance was consistent despite the predation event. We also found that the conditional modes generated from the post-predation trials were consistent with the conditional modes reported in (29) (visual tolerance correlation: (r(14) = .80, p = 0.001); displacement tolerance correlation: (r(14) = .68, p < 0.001)) despite the previous study utilising an additional 12 approaches (for each individual) from another observer differing in physical characteristics and familiarity with the study animals.

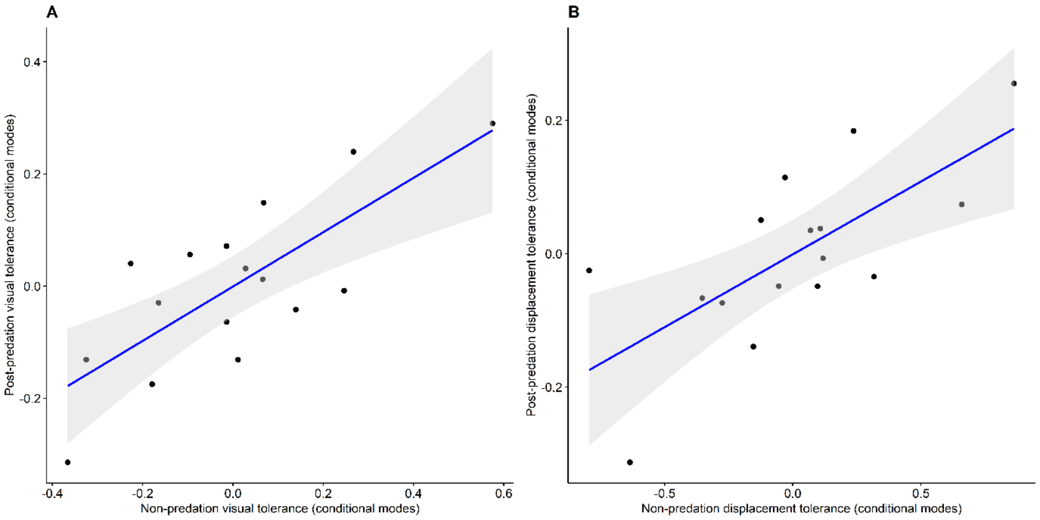

Fig 3. Non-predation and post-predation correlations for conditional modes of each tolerance measure: (a) correlation between individual-level visual tolerance estimates (derived from VOD measures); (b) correlation between individual-level displacement tolerance estimates (derived from FID measures). Lower/negative estimates indicate greater tolerance. Conditional modes for non-predation data were calculated from the non-predation models, and post-predation conditional modes from the post-predation models.

Discussion

We examined the visual orientation and flight responses of habituated chacma baboons to approaches made by observers, comparing responses from after a leopard predation event to data collected during less threatening and stressful scenarios. The predation event had little effect on either variable or individual tolerance estimates. However, some minor effects were discernible - the predation event seemed to make individuals slightly nervous (quicker visual orientation) for a short period - but this seemed to return to a normal level during subsequent trials. Furthermore, even though visual orientation was initially quicker, FIDs were largely unchanged following the predation, suggesting the baboons still viewed observers as a high-level social threat and that this was unaltered despite being slightly more primed to detect threats shortly after the predation event. Although derived from a single predation event these results suggest that human approaches (using FID methodology) measure a very specific threat perception relating to humans when animals have experienced habituation processes and most of their human encounters are benign. As such, FIDs may not be generalisable to other forms of risk (i.e., predation) once habituation processes are underway.

Due to the intensity of the predation event, the subsequent alarm state in the study group, and the time needed to formulate an effective study design, our first approach took place 49 minutes after the predation event - 10 minutes after we considered the alarm state to have mostly subsided. It is possible that if approaches were commenced immediately after the predation event, then our results may have been different, although the ethical and safety implications of undertaking such approaches made it unfeasible. Nevertheless, Engh et al (48) reported that female chacma baboons who lost a relative had increased faecal glucocorticoid levels in the four weeks that followed predation events relative to baseline levels, before returning to baseline levels in the subsequent month. Although the observed increase could be attributed to a loss of a social partner, these females adapted to the loss by increasing their grooming time and diversifying the number of grooming partners. As such, it was interpreted that the physiological stress endured due to a loss of a relative was likely mitigated by the behavioural adjustments, suggesting the increase in glucocorticoid levels was partly due to lingering effects of the predation directly. In gray-cheeked mangabeys (*Lophocebus albigena*) it was found that males generally exhibited increased cortisol levels the day after encounters with crowned eagles (49), whilst the stress response of captive chimpanzees to anaesthesia resulted in increased faecal cortisol concentrations for two days post stress stimulus (50). It seems likely, therefore, that our study animals experienced heightened stress levels for the duration of our post-predation approaches and so the lack changes in VOD and FID is unlikely to be because trials began too long after the predation event.

Some individuals may have found the event more stressful than others due to witnessing the event directly (or at least detecting the leopard), whilst others may have had stronger social connections with the predated animal (48). Although these factors could not be explored formally in this study, we did observe that several individuals who were present at the predation site before our arrival appeared incredibly agitated for some time after the event (alarm barks continued after leaving the predation site). Despite this, individual VODs and FIDs remained relatively consistent, whilst individual tolerance estimates (assessed using conditional modes) were also relatively consistent for most individuals.

Despite their tolerance of observers and finding no detectable differences in responses to familiar or unfamiliar observers previously (29), the habituated baboons consistently fled at the site of workers from a local farm (often without a behavioural driver such as chasing or throwing stones by the workers). This suggests that even in relatively stable settings where human-primate interactions are normally benign, that baboons still distinguish between classes of humans and their potential risks. In addition, the habituated group still exhibited intense alarm and agonistic responses (e.g., chase and attack) to foreign individuals/groups of baboons and leopards, rock pythons, and crowned eagles (*AA, personal observations*); strongly suggesting there was no evidence of habituation transfer in this group. Individuals in hunted and non-hunted primate populations can apparently distinguish between human groups (e.g., hunters, gatherers, researchers) and display diminished responses to lower threats, such as researchers (51). This implies that FID researchers would need to carefully mimic the appearance and behaviour of hunters to generate true indications of hunting pressure, at least in wild primates, although other species have been shown to discriminate between human stimuli, e.g., snorkelers vs spearfishers in fishes (52) and familiar vs unfamiliar human stimuli in Asian elephants (*Elephas maximus*) (53). Some caution may need to be applied however, as FID research also indicates strong habituation effects to FID approaches (54); thus, in species that struggle to differentiate between human stimuli, habituation to FID approaches could also enhance hunting success.

Thought must also be given to landscape level habituation, such as proximity to camps, trails, recreational areas etc, and how it can interact with individual-level habituation to FID methodology. For example, Petelle et al (54) reported reduced FIDs in *M.flaviventris* colonies that typically received greater anthropogenic disturbance, whilst also reporting that individual FIDs decreased with increasing trial number for both yearlings and adults across all colonies; indicating two distinct habituation processes had influenced the FIDs of study animals. Results such as these highlight numerous dimensions to habituation/sensitization processes that need to be measured to capture the true impact of approach methodology and understand the fear perception individual animals have towards multiple human stimuli (e.g., (29)).

Outside of direct observations on habituated animals, anthropogenic disturbance is likely to vary in type (e.g., hunter, researcher, tourists etc), intensity (i.e., consistent, sporadic, rare), and outcome (i.e., benign, life-threatening), all of which could vary temporally at the individual-level. As a result, habituation/sensitization process are likely to be ongoing in most wild animals (55). Investigating individual consistency through time should be an important avenue for future research to explore; however, care must be taken to ensure approaches do not engineer phenotypes that are more vulnerable to human-wildlife conflict and hunting.

Although we present data from a single group and after only one predation event, the 192 non-predation trials (12 approaches per individual) is beyond the norm in FID research (in terms of individual sampling effort), whilst our 48 post-predation observations (3 approaches per individual) is similar to sample sizes in the small number of studies that have achieved multiple approaches on known individuals (36, 56, 57). highlight that our previous study (29) demonstrated the individual consistency in VOD and FID measurements for this study group of baboons (69 individuals received 24 trials each, n = 1656 total trials) across a range of environmental (e.g., habitat type), social (e.g., number of neighbours), and methodological scenarios (e.g., observer familiarity, trial number), across multiple years (58). While future research following other opportunistic predation events would be beneficial, the broader research surrounding our current results adds confidence to our findings.

Typically, FID research has explored anthropogenic disturbance and risk hypotheses on dichotomous landscape level axis, such as urban vs non-urban areas (59). Elsewhere, inferences about FIDs have been made based on observations from inside vs outside protected areas (60), or across areas varying in predation pressure (61). Experimental designs have also been used to monitor the long-term FID responses of different groups of animals released into exclosures with and without predators (62) and to compare FIDs of animals across anthropogenic disturbance gradients in response to typical human stimuli and to novel predators (63). Our results offer a preliminary perspective on different axis, exploring how individual VODs and FIDs are modified immediately after encountering a natural predator. Although our study utilised a naturally occurring event, a similar approach could be used to track individual responses to experimental predator encounters, habitat modifications, or changes in anthropogenic disturbances, and would be an effective way of tackling outstanding FID questions. For example, assessing individual FIDs in rural settings prior to urbanisation could reveal whether intolerant individuals habituate to anthropogenic disturbance or whether urbanisation selects for more tolerant or bolder phenotypes (27).

In the non-predation dataset used in this study, the least tolerant animals had an average VOD of 6.17 meters and an average FID of 5.01 meters. It is clear therefore that our study group was well habituated. Even so, some individuals were still less tolerant than examples reported elsewhere in FID research. For example, the lowest FID distance for burrowing owls was 4m in (56) and 3.5m in (57), average FIDs of 1m were reported in some populations of European birds (11), several bird species had average FIDs of less than 5 meters in eastern Australia and Tasmania (1), whilst some agama lizards (*Agama planiceps*) (47) and coral reef fishes (61) allowed approaches to within half a meter. As such, the habituation level of baboons is unlikely to beyond the capacity for other species, suggesting our results should be applicable to animals that have begun habituation processes as a result of urbanisation, tourism, or any other consistent but benign exposure to humans. Future FID research should attempt to integrate repeated approaches on a diverse range of individually identifiable phenotypes to ensure that assessments of fear perception are not biased by oversampling individuals within particular tolerances towards humans, allowing greater insights into whether FID approaches truly capture general risk perception in all scenarios.

In conclusion, our results suggest habituated chacma baboons display individual tolerance levels (towards observers) that are consistent even after predation events. Most FID research has so far worked on the assumption that humans are considered equivalent to predators (14), but, in an ever-urbanising world this may only rarely be the case. Future FID studies will need to take care when assuming their approaches are measuring other types of perceived risk, as our results suggest FID methods may only measure very specific types of human-risk when habituation has taken place. Given the variability in individual tolerances (29), future work utilising human approaches will need to incorporate an individual-level focus to truly ascertain the anthropogenic impact of the study methodology and how it interacts with other forms of ongoing anthropogenic disturbance. In such scenarios FIDs may not represent all forms of risk perception, but carefully designed studies could improve our understanding of the impact humans have on animals in a range of scenarios.

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Data accessibility

All necessary data required to produce all analyses reported in this article will be uploaded to dryad or as supplementary information if accepted for publication.

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References

1. D. T. Blumstein, Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* **67**, 852–857 (2003).
2. D. T. Blumstein, L. L. Anthony, R. Harcourt, G. Ross, Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biol. Conserv.* **110**, 97–100 (2003).
3. D. L. Cheney, R. W. Wrangham, “Predation” in *Primate Societies*, 1st Ed., B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (University of Chicago Press, 1987), pp. 227–239.
4. L. A. Isbell, Predation on Primates: Ecological Patterns and Evolutionary Consequences. *Evol. Anthropol.* **3**, 61–71 (1994).
5. S. Lingle, Anti-Predator Strategies and Grouping Patterns in White-Tailed Deer and Mule Deer. *Ethology* **107**, 295–314 (2001).
6. W. E. Cooper, Variation in Escape Behavior among Individuals of the Striped Plateau Lizard *Sceloporus virgatus* May Reflect Differences in Boldness. *J. Herpetol.* **43**, 495–502 (2009).
7. W. E. Cooper, W. G. Frederick, Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67 (2007).
8. W. E. Cooper, D. S. M. Samia, D. T. Blumstein, FEAR, spontaneity, and artifact in economic escape theory: A review and prospectus. *Adv. Study Behav.* **47**, 147–179 (2015).
9. R. C. Ydenberg, L. M. Dill, The Economics of Fleeing form Predators. *Adv. study Behav.* **16**, 229–249 (1986).
10. W. E. Cooper, W. G. Frederick, Predator lethality, optimal escape behavior, and autotomy. *Behav. Ecol.* **21**, 91–96 (2010).
11. M. Díaz, *et al.*, The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape Distances of Birds across Europe. *PLoS One* **8**, e64634 (2013).
12. D. S. M. Samia, F. Nomura, D. T. Blumstein, Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* **9**, 1–4 (2013).
13. T. Stankowich, D. T. Blumstein, Fear in animals: A meta-analysis and review of risk assessment. *Proc. R. Soc. B Biol. Sci.* **272**, 2627–2634 (2005).
14. A. Frid, L. M. Dill, Human-caused disturbance stimuli as a form of predation risk. *Ecol. Soc.* **6**, 11 (2002).
15. T. H. Setsaas, T. Holmern, G. Mwakalebe, S. Stokke, E. Røskaft, How does human exploitation affect impala populations in protected and partially protected areas? - A case study from the Serengeti Ecosystem, Tanzania. *Biol. Conserv.* **136**, 563–570 (2007).
16. R. Sreekar, E. Goodale, R. D. Harrison, Flight initiation distance as behavioral indicator of hunting pressure: A case study of the Sooty-headed Bulbul (*Pycnonotus aurigaster*) in Xishuangbanna, SW China. *Trop. Conserv. Sci.* **8**, 505–512 (2015).

17. D. T. Blumstein, “Attention, habituation, and antipredator behaviour: implications for urban birds” in *Avian Urban Ecology*, D. Gil, H. Brumm, Eds. (Oxford University Press, 2014), pp. 41–53.

18. M. Carrete, J. L. Tella, Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS One* **6(4)**, 1–8 (2011).

19. A. P. Møller, P. Tryjanowski, Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behav. Ecol.* **25**, 960–966 (2014).

20. F. Morelli, *et al.*, Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecol. Evol.* **9**, 6096–6104 (2019).

21. F. Morelli, *et al.*, Escape behaviour of birds in urban parks and cemeteries across Europe: Evidence of behavioural adaptation to human activity. *Sci. Total Environ.* **631**–**632**, 803–810 (2018).

22. D. S. M. Samia, S. Nakagawa, F. Nomura, T. F. Rangel, D. T. Blumstein, Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* **6** (2015).

23. M. M. McGowan, P. D. Patel, J. D. Stroh, D. T. Blumstein, The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology* **120**, 1–9 (2014).

24. R. A. Mccleery, Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landsc. Ecol.* **24**, 483–493 (2009).

25. C. Li, R. Monclús, T. L. Maul, Z. Jiang, D. T. Blumstein, Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Appl. Anim. Behav. Sci.* **129**, 146–152 (2011).

26. M. V. Price, E. H. Strombom, D. T. Blumstein, Human activity affects the perception of risk by mule deer. *Curr. Zool.* **60**, 693–699 (2014).

27. B. Geffroy, D. S. M. Samia, E. Bessa, D. T. Blumstein, How Nature-Based Tourism Might Increase Prey Vulnerability to Predators. *Trends Ecol. Evol.* **30**, 755–765 (2015).

28. A. P. Møller, Urban areas as refuges from predators and flight distance of prey. *Behav. Ecol.* **23**, 1030–1035 (2012).

29. A. T. L. Allan, A. L. Bailey, R. A. Hill, Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Sci. Adv.* **6**, eaaz0870 (2020).

30. A. L. de Raad, R. A. Hill, Topological spatial representation in wild chacma baboons (*Papio ursinus*). *Anim. Cogn.* **22**, 397–412 (2019).

31. C. Howlett, J. M. Setchell, R. A. Hill, R. A. Barton, The 2D : 4D digit ratio and social behaviour in wild female chacma baboons (*Papio ursinus*) in relation to dominance, aggression, interest in infants, affiliation and heritability. *Behav. Ecol. Sociobiol.* **69**, 61–74 (2015).

32. K. S. Williams, S. T. Williams, L. E. Fitzgerald, E. C. Sheppard, R. A. Hill, Brown hyaena and leopard diets on private land in the Soutpansberg Mountains , South Africa. *Afr. J. Ecol.* **56**, 1021–1027 (2018).

33. J. N. Chase Grey, S. Bell, R. A. Hill, Leopard diets and landowner perceptions of human wildlife conflict in the Soutpansberg Mountains , South Africa. *J. Nat. Conserv.* **37**, 56–65 (2017).

34. F. Dumont, C. Pasquaretta, D. Réale, G. Bogliani, A. von Hardenberg, Flight Initiation Distance

and Starting Distance: Biological Effect or Mathematical Artefact? *Ethology* **118**, 1051–1062 (2012).

35. D. T. Blumstein, D. S. M. Samia, T. Stankowich, W. E. Cooper, “Best practice for the study of escape behavior” in *Escaping from Predators: An Integrative View of Escape Decisions*, W. E. Cooper, D. T. Blumstein, Eds. (Cambridge University Press, 2015), pp. 405–419.

36. A. M. Runyan, D. T. Blumstein, Do individual differences influence initiation distance? *J. Wildl. Manage.* **68**, 1124–1129 (2004).

37. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).

38. A. T. L. Allan, R. A. Hill, Definition and interpretation effects: How different vigilance definitions can produce varied results. *Rev.*

39. N. C. Bonnot, *et al.*, Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).

40. P.-C. Bürkner, brms : An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

41. A. Gelman, A. Jakulin, M. G. Pittau, Y. S. Su, A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.* **2**, 1360–1383 (2008).

42. N. P. Lemoine, *et al.*, Underappreciated problems of low replication in ecological field studies. *Ecology* **97**, 2554–2561 (2016).

43. N. P. Lemoine, Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* **128**, 912–928 (2019).

44. J. Ghosh, Y. Li, R. Mitra, On the Use of Cauchy Prior Distributions. *Bayesian Anal.* **13**, 359–383 (2018).

45. J. Gabry, D. Simpson, A. Vehtari, M. Betancourt, A. Gelman, Visualization in Bayesian workflow. *J. R. Stat. Soc. Ser. A Stat. Soc.* **182**, 389–402 (2019).

46. R. McElreath, *Statistical Rethinking 2: A Bayesian Course with Examples in R and Stan*, Second (2019).

47. A. J. Carter, R. Heinsohn, A. W. Goldizen, P. A. Biro, Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* **83**, 1051–1058 (2012).

48. A. L. Engh, *et al.*, Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc. R. Soc. B Biol. Sci.* **273**, 707–712 (2006).

49. M. E. Arlet, L. A. Isbell, Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* **63**, 491–499 (2009).

50. P. L. Whitten, R. Stavisky, F. Aureli, E. Russell, Response of fecal cortisol to stress in captive chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **44**, 57–69 (1998).

51. S. Papworth, E. J. Milner-Gulland, K. Slocombe, Hunted Woolly Monkeys (*Lagothrix poeppigii*) Show Threat-Sensitive Responses to Human Presence. *PLoS One* **8(4)**, 1–11 (2013).

52. V. Sbragaglia, *et al.*, Spearfishing modulates flight initiation distance of fishes: The effects of protection, individual size, and bearing a speargun. *ICES J. Mar. Sci.* **75**, 1779–1789 (2018).

53. E. J. Polla, C. C. Grueter, C. L. Smith, Asian Elephants (*Elephas maximus*) Discriminate Between Familiar and Unfamiliar Human Visual and Olfactory Cues. *Anim. Behav. Cogn.* **5**, 279–291 (2018).

54. M. B. Petelle, D. E. McCoy, V. Alejandro, J. G. A. Martin, D. T. Blumstein, Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**, 1147–1154 (2013).

55. D. T. Blumstein, Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.* **120**, 255–262 (2016).

56. M. Carrete, J. L. Tella, Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**, 167–170 (2010).

57. M. Carrete, J. L. Tella, High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Sci. Rep.* **3**, 1–7 (2013).

58. A. T. L. Allan, A. White, R. A. Hill, Intolerant baboons avoid observer proximity, creating biased inter-individual association patterns. *Rev.*

59. K. Uchida, K. Suzuki, T. Shimamoto, H. Yanagawa, I. Koizumi, Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. *J. Zool.* **298**, 225–231 (2016).

60. K. M. Gotanda, K. Turgeon, D. L. Kramer, Body size and reserve protection affect flight initiation distance in parrotfishes. *Behav. Ecol. Sociobiol.* **63**, 1563–1572 (2009).

61. F. A. Januchowski-Hartley, N. A. J. Graham, D. A. Feary, T. Morove, J. E. Cinner, Fear of fishers: Human predation explains behavioral changes in coral reef fishes. *PLoS One* **6**, e22761 (2011).

62. R. West, M. Letnic, D. T. Blumstein, K. E. Moseby, Predator exposure improves anti-predator responses in a threatened mammal. *J. Appl. Ecol.* **55**, 147–156 (2018).

63. I. Rodriguez-Prieto, E. Fernández-Juricic, J. Martín, Y. Regis, Antipredator behavior in blackbirds: Habituation complements risk allocation. *Behav. Ecol.* **20**, 371–377 (2009).

Supporting information

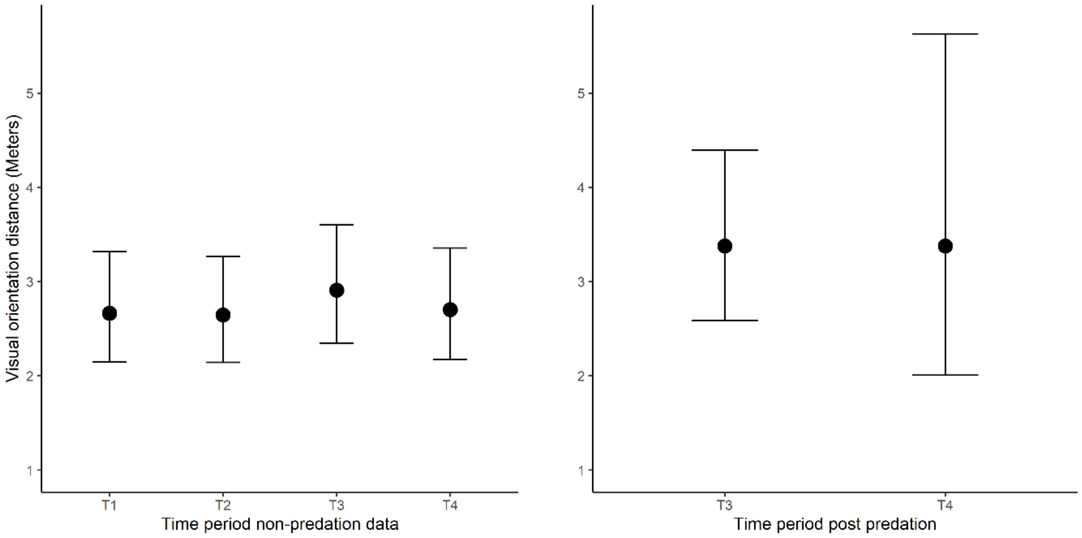

Fig S1. Mean conditional effects for visual orientation distance and time period, panel (a) represents non-predation data, whilst panel (b) represents post-predation data.

The mean VOD conditional effect (see fig S1) of time periods 3 and 4 for non-predation data were 2.89 (2.34,3.59) and 2.69 (2.16,3.33). Whilst the respective information for post-predation data was 3.38 (2.59,4.39) and 3.38 (2.01,5.63), representing a mean conditional effect difference of 49cm and 69cm (between non-predation data and post-predation data) for time period 3 and 4 respectively.

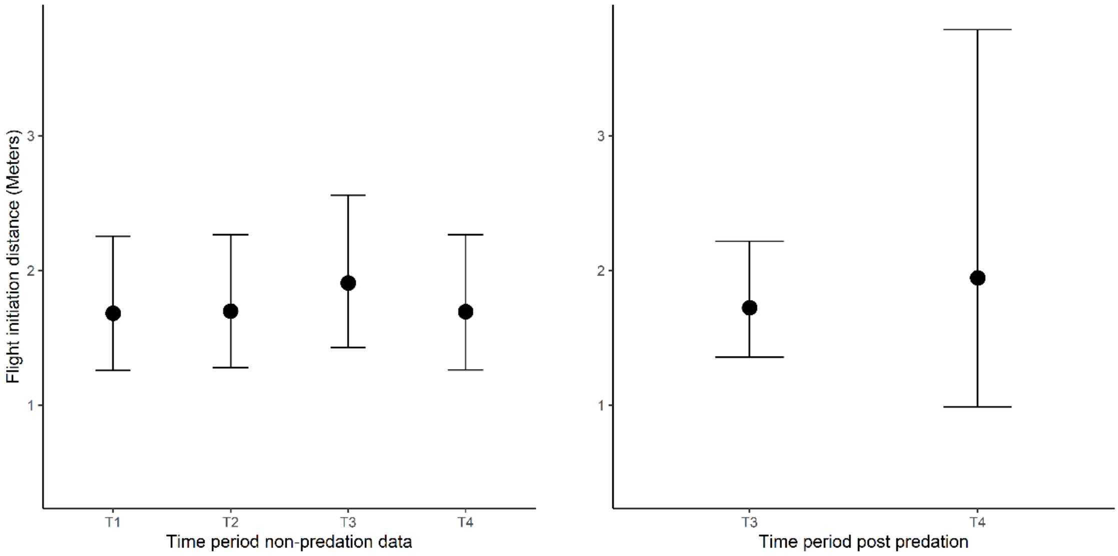

Fig S2. Mean conditional effects for flight initiation distance and time period, panel (a) represents non-predation data, whilst panel (b) represents post-predation data.

The mean FID conditional effect (see fig S2) of time periods 3 and 4 for non-predation data were 1.91 (1.42,2.56) and 1.69 (1.25,2.27). Whilst the respective information for post-predation data was 1.72 (1.35,2.22) and 1.94 (0.98,3.79), as a result, the post-predation mean conditional effect for time period 3 was 19cm lower than non-predation data, whilst post-predation was 25cm higher than the non-predation data for time period 4.

Table S1. VOD model summary for non-predation data. Parameter estimates for the model describing the relationship between VOD and the predictor variables. CI, credible interval.

Population-Level Effects:	**Estimate**	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	1.06	0.11	0.83	1.28	1.00	17425	16706
Visual orientation distance delay (VODD)	-0.05	0.04	-0.13	0.03	1.00	14112	14728
Compatibility (Looking)	0.04	0.05	-0.06	0.14	1.00	31632	19128
Compatibility (Not looking not engaged)	0.01	0.08	-0.15	0.16	1.00	25503	18582
Habitat (Open)	0.27	0.05	0.17	0.36	1.00	26782	18678
Number of neighbours in 5m	-0.02	0.02	-0.05	0.02	1.00	32494	18920
Time period (2)	-0.01	0.06	-0.13	0.11	1.00	26318	19642
Time period (3)	0.09	0.06	-0.03	0.21	1.00	28963	19481
Time period (4)	0.01	0.06	-0.11	0.14	1.00	22580	18159
Trial number	0	0.01	-0.01	0.02	1.00	25632	19227
Family Specific Parameters:							
sigma	0.28	0.02	0.25	0.31	1.00	17237	16861
Group-Level Effects:							
Individual identity (16 levels)							
sd(Intercept)	0.32	0.09	0.18	0.52	1.00	12070	16101
sd(VODD)	0.12	0.04	0.05	0.22	1.00	6637	8884
sd(TrialNo)	0.01	0.01	0	0.02	1.00	12782	13823
cor(Intercept,VODD)	-0.15	0.33	-0.7	0.58	1.00	8601	11062
cor(Intercept,TrialNo)	-0.01	0.48	-0.86	0.87	1.00	29082	17931
cor(VODD,TrialNo)	-0.04	0.49	-0.88	0.85	1.00	24454	18840

Table S2. VOD model summary for post-predation data. Parameter estimates for the model describing the relationship between VOD and the predictor variables. CI, credible interval.

Population-Level Effects:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	1.48	0.19	1.1	1.86	1.00	15054	17112
Visual Orientation Distance Delay (VODD)	-0.11	0.11	-0.33	0.09	1.00	11627	13721
Compatibility (Looking)	0.17	0.16	-0.13	0.48	1.00	15486	17269
Compatibility (Not engaged not looking)	0.05	0.18	-0.31	0.41	1.00	19931	18047
Habitat (Open)	-0.06	0.15	-0.35	0.24	1.00	16406	17308
Number of neighbours within 5m	-0.07	0.04	-0.15	0.02	1.00	17237	17283
Time period 4	0	0.21	-0.42	0.42	1.00	11925	14527
Trial Number 2 post predation	-0.09	0.14	-0.37	0.2	1.00	12759	16386
Trial Number 3 post predation	-0.21	0.26	-0.71	0.29	1.00	12330	14631
Family Specific Parameters:							
shape	21.04	21.1	7.26	72.98	1.00	1468	1152
Group-Level Effects:							
Individual identity (16 levels)							
sd(Intercept)	0.28	0.16	0.02	0.64	1.00	3490	8283
sd(VODD)	0.18	0.1	0.02	0.39	1.00	3861	6953
sd(TrialNoTrial2)	0.18	0.13	0.01	0.49	1.00	3453	6528
sd(TrialNoTrial3)	0.21	0.14	0.01	0.52	1.00	3214	7440
cor(Intercept,VODD)	-0.09	0.44	-0.82	0.77	1.00	7999	14009
cor(Intercept,TrialNoTrial2)	-0.26	0.44	-0.9	0.69	1.00	8544	16568
cor(VODD,TrialNoTrial2)	-0.03	0.43	-0.81	0.78	1.00	15736	17351
cor(Intercept,TrialNoTrial3)	-0.11	0.43	-0.83	0.74	1.00	11569	14760
cor(VODD,TrialNoTrial3)	-0.24	0.42	-0.89	0.67	1.00	11981	16686
cor(TrialNoTrial2,TrialNoTrial3)	0.11	0.45	-0.77	0.85	1.00	11261	18084

Table S3. FID model summary for non-predation data. Parameter estimates for the model describing the relationship between FID and the predictor variables. CI, credible interval.

Population-Level Effects:	**Estimate**	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	0.66	0.16	0.35	0.97	1.00	6975	12546
Visual orientation distance index (VODI)	-0.13	0.05	-0.23	-0.03	1.00	15903	15256
Engaged (Not engaged)	0.07	0.06	-0.04	0.18	1.00	31451	18530
Habitat (Open)	0.22	0.06	0.11	0.33	1.00	30976	19003
Number of neighbours in 5m	-0.06	0.02	-0.1	-0.01	1.00	24852	18340
Time period (2)	0.01	0.08	-0.14	0.16	1.00	19478	18357
Time period (3)	0.13	0.08	-0.03	0.27	1.00	20021	18781
Time period (4)	0.01	0.08	-0.14	0.16	1.00	20437	18687
Trial number	0	0.01	-0.01	0.02	1.00	22816	17929
Family Specific Parameters:							
sigma	0.35	0.02	0.31	0.39	1.00	20819	17377
Group-Level Effects:							
Individual identity (16 levels)							
sd(Intercept)	0.5	0.12	0.3	0.79	1.00	8819	11872
sd(VODI)	0.11	0.06	0.01	0.25	1.00	5708	6980
sd(TrialNo)	0.01	0.01	0	0.03	1.00	9067	10206
cor(Intercept,VODI)	0.22	0.39	-0.55	0.89	1.00	14389	12983
cor(Intercept,TrialNo)	-0.28	0.46	-0.93	0.73	1.00	20596	16315
cor(VODI,TrialNo)	-0.23	0.48	-0.93	0.78	1.00	14801	18491

Table S4. FID model summary for post-predation data. Parameter estimates for the model describing the relationship between FID and the predictor variables. CI, credible interval.

Population-Level Effects:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercept	0.33	0.21	-0.07	0.75	1.00	13782	17143
Visual Orientation Distance Index (VODI)	0.23	0.1	0.03	0.43	1.00	13948	15853
Engaged (Not engaged)	0.29	0.16	-0.01	0.6	1.00	11678	15621
Habitat (Open)	-0.05	0.15	-0.33	0.25	1.00	15930	17451
Number of neighbours within 5m	-0.09	0.05	-0.18	0	1.00	11852	15558
Time period 4	0.12	0.32	-0.49	0.76	1.00	8192	10022
Trial Number 2 post predation	-0.05	0.19	-0.44	0.31	1.00	10779	10083
Trial Number 3 post predation	-0.31	0.34	-0.99	0.36	1.00	9091	10542
Family Specific Parameters:							
shape	14.03	14.54	5.61	42.82	1.00	2061	1502
Group-Level Effects:							
Individual identity (16 levels)							
sd(Intercept)	0.24	0.15	0.02	0.57	1.00	4313	8130
sd(VODI)	0.09	0.08	0	0.29	1.00	6188	8417
sd(TrialNoTrial2)	0.36	0.22	0.02	0.83	1.00	2877	6859
sd(TrialNoTrial3)	0.17	0.13	0.01	0.47	1.00	4606	6321
cor(Intercept,VODI)	-0.15	0.46	-0.88	0.76	1.00	19464	16743
cor(Intercept,TrialNoTrial2)	-0.06	0.42	-0.79	0.77	1.00	9945	14897
cor(VODI,TrialNoTrial2)	-0.02	0.43	-0.8	0.79	1.00	9339	14873
cor(Intercept,TrialNoTrial3)	-0.08	0.44	-0.83	0.78	1.00	20489	17746
cor(VODI,TrialNoTrial3)	-0.06	0.45	-0.84	0.78	1.00	16192	16930
cor(TrialNoTrial2,TrialNoTrial3)	0.12	0.44	-0.75	0.85	1.00	15488	19574

Chapter 6. Investigating whether inter-individual differences in tolerance lead to observer-governed phenotypic assortment

Intolerant baboons avoid observer proximity, creating biased inter-individual association patterns.

Authors: Andrew T. L. Allan, Amy White, & Russell A. Hill

AA conceived and coordinated the study, carried out statistical analysis, and drafted the initial manuscript. AW coded behavioural data from videos, participated in study design and statistical analysis, and critically revised the manuscript. RH participated in study design, statistical analysis, and critically revised the manuscript.

Abstract

Social network analysis is an increasingly popular tool for behavioural ecologists exploring the social organisation of animal populations. Such analyses require data on inter-individual association patterns, which in wild populations are often collected using direct observations of habituated animals. This assumes observers have no influence on animal behaviour. Our previous work showed that individuals in a habituated group of chacma baboons (*Papio ursinus griseipes*) displayed consistent and individually distinct responses to observer approaches. We explored the implications of this by measuring the inter-individual association patterns of the same group of chacma baboons at different observer distances. Using mixed-model analysis, we found a strong positive association between individual tolerance levels (towards observers) and how often an animal appeared as a neighbour to focal animals when observers were nearer, i.e., tolerant animals were over sampled when the observer was closer. When the observer was further away, there was a neutral relationship between the same variables. This appears to be the first empirical evidence that observer presence and behaviour can influence the association patterns of habituated animals and thus have potentially significant impacts on measured social networks. Tolerance and observer factors therefore need addressing in future work using direct observations on wild animals.

Significance statement

Social network analysis is a popular tool for exploring the social organisation of animal populations. Often, behavioural ecologists sample this information using direct observations of habituated animals, typically assuming observers do not influence inter-individual association patterns. We previously demonstrated that a group of wild habituated chacma baboons had substantial variation between individuals in their tolerance of researchers, with some animals consistently tolerant of observer proximity whereas others exhibited greater avoidance despite years of observation. Here, using the same group of baboons (*Papio ursinus griseipes*), we highlight the significant implication of this: tolerant animals were over sampled when the observer was closer, suggesting tolerance and observer effects may bias analyses of inter-individual association patterns and social networks, and require consideration in future research using direct observations on wild animals.

Introduction

In behavioural ecology research, habituation processes have been used to reduce the fear animals have towards humans, allowing behavioural data to be collected directly (1). An expansive body of literature suggests this process is robust to potential issues; however, direct observations of habituated animals contain two implicit assumptions that are rarely acknowledged or tested empirically. Firstly, that observers have a neutral effect on study animals, and secondly, that all study animals are habituated equally (2). We found evidence that neither assumption was valid in a habituated group of chacma baboons, with observers viewed as equivalent to a high-level social threat and while tolerance of observers was consistent within individuals it was distinct between them (2). These findings open up a range of new questions regarding how the presence of such a trait impacts the behaviour and ecology of habituated animals.

Observer neutrality has only received minor discussion in species often exposed to direct observations such as primates (1, 3, 4) and meerkats (5), although observer effects on the behaviour of habituated animals have been reported elsewhere. Habituated bat-eared foxes (*Octocyon megalotis*) were found to increase vigilance during the beginning phases of focal observations (6) suggesting that habituation had not led to complete observer neutrality and some fear of humans remained. In reef fishes, cleaning interactions between individuals were found to be more frequent when divers (observers) were absent, despite a long history of diver presence in the area (7). If observers have a similar effect on other habituated animals and inter-individual differences in tolerance remain once habituation processes are deemed to be completed, then observer-governed effects could have fundamentally biased our understanding of a range of behaviours across the animal kingdom.

Characterising the social systems of animals is often attempted through sampling inter-individual association patterns, such as affiliative and agonistic interactions, or spatial proximity between individuals (8). Over the last decade, social network analysis has become an increasingly popular tool for visualising and analysing these types of data (9) and has been used to explore a number of broad themes, including the fitness consequences of sociality, identifying individual social roles within groups, and mapping disease transmission in wild populations (10, 11). Sampling inter-individual association patterns directly is reliant upon the assumption that observers do not impact on social interactions, yet observer effects appear mostly overlooked. Recent research has shown that humans can influence typical patterns of social relationships in wild primates (12), whilst there is concern amongst researchers that observers are unlikely to ever become a neutral stimulus and the presence of unhabituated behaviours may undermine the validity of data (13). The presence of a tolerance trait (i.e., (2)) would also indicate that both observer presence and behaviour (e.g., distance to animals, observer movement etc.) could lead to observer-governed phenotypic assortment, with intolerant animals adjusting their spatial position to avoid the observer. Such an effect would undoubtedly bias inter-individual association patterns as intolerant phenotypes may be under-sampled relative to tolerant animals.

Here we explore the implications of individual variation in tolerance and test whether observer proximity can influence inter-individual association patterns in a group of habituated chacma baboons. Baboon association patterns have been sampled using a range of proximity measures and affiliative interactions (14–16), however, different sampling methods can produce different networks (14). Despite this, there has been little discussion of whether association patterns can be affected by observer presence and behaviour during direct observations. To address this, we recorded the proximity associations of all group members and explored whether the interaction between individual tolerance (of each baboon towards the observer) and observer distance influenced how often each individual was sampled in proximity of focal animals, and whether the hypothesized trends were consistent across different years. If intolerant individuals avoided observers, we predicted that intolerant phenotypes would be sampled as often as other individuals when the observer was further away but be sampled less often when the observer was close. If confirmed, this would have important implications for future studies based on social networks and inter-individual association patterns.

Methods

This research was undertaken under ZA/LP/81996 research permit, with ethical approval from the Animal Welfare Ethical Review Board (AWERB) at Durham University. All inter-individual association data was collected between June 2018 and June 2019 on a wild habituated group of Afro-montane chacma baboons in the western Soutpansberg Mountains, South Africa (central coordinates S29.44031°, E23.02217°) (for study site description see (2)).

Study group

The study group was habituated circa 2005 and was the focus of intermittent research attention until 2014. The study area experienced long-term anthropogenic activities (local farming, forestry, and residences) prior to 2005, as such, consistent interactions with humans have been ongoing with this population for some time. From 2007 onwards numerous researchers were able to collect expansive datasets on the study group (e.g., (17, 18), indicating that habituation was at a typical level found elsewhere (also validated by AA and RH, who had researched chacma baboons elsewhere). From 2014 the group received full day (dawn until dusk) follows 3 to 4 days a week, with occasional gaps of up to 5 weeks in duration. The follow schedule was designed to ensure that the study group retained as much of their natural interactions with predators as possible.

The study site was located in a private nature reserve and the study group was not hunted during observation gaps or engaged in any conflict with humans, other than occasionally being scared (chasing, yelling, throwing stones etc) from a small plantation by local workers, usually resulting in alarm barks and fleeing responses. However, the study group appeared adept at recognising the differences between researchers and these threats (19). The majority of the study group's home-range typically overlapped with the core area of the Lajuma Research Centre, and as a result, interactions with staff living in the area, unfamiliar researchers, and tourists were frequent. However, the baboons had not engaged in 'raiding' residences, threatening humans, or any other potentially negative symptom of habituation before the end of this study. During this study the group contained between 85 and 100 individuals.

Sampling methodology for proximity associations

30-second focal sampling was used to collect proximity associations between all group members (excluding infants). All data was collected between June 2018 and June 2019; the majority of 2018's data was collected during the wet season, whilst most of 2019's data was collected during the dry season. To account for time of day, each day was split into four time-periods that were seasonally adjusted ensuring each period accounted for 25% of the current day length. A randomly ordered list of individuals was produced for each day, the first individual identified from the top 15 (approx. 20% of group size) individuals on the list was sampled immediately. A video camera was used by AA to record all focal observations (Panasonic HC-W580 Camcorder). At the end of the 30-second focal observation the identities of all neighbouring conspecifics within 5 meters, 2.5m, 1m, and touching the focal animal were recorded (audibly by AA). We chose the end of the focal observation to record this data as this was most likely to reflect the conditions during the focal, i.e., the observer had been in proximity for at least 30 seconds.

Neighbour information was extracted from video footage and entered manually by AA and AW. Data was split into two years to understand whether there was consistency in the hypothesized effects through time and to reflect underlying differences in environmental conditions during the two study periods; during the dry season (2019 data) fruits and seeds are scarce and day lengths are several hours shorter than the wet season such that day journey lengths are often shorter than the wet season and animals are much more sedentary which could impact inter-individual spacings. In 2018 each individual was sampled between 28 and 30 times; 28 focals were randomly selected from each individual to make sampling even. For 2019 there were between 25 and 27 focals; 25 samples of each individual were randomly selected. Observations were undertaken at a range of distances. For both years the median end observer distance was 4.5m; data was thus split into close focal observations of less than or equal to 4.5m (2018: n=920, 2019: n=816), and observations greater than 4.5m (2018: n=928, 2019: n=810).

Flight initiation distance procedure

Individual displacement tolerance estimates were previously quantified in (2) using a flight initiation distance (FID) procedure (20) that was completed between October 2017 and April 2018, prior and independent to the commencement of proximity association focal sampling in June 2018. Individual baboons were approached by an observer, and the distance at which the animal displaced away from the observer measured. This procedure was repeated 24 times for each individual baboon, with approaches spread evenly across two observers differing in familiarity. To ensure the data collected from 2017/2018 FID approaches were applicable to focal data collected throughout 2018 and 2019 we tested a further 15 individuals (approximately 25% of the group) beginning two weeks after the proximity focals were completed (late June 2019). We tested the effect of year on individual tolerance estimates and found them to be consistent across years (see supporting information text S1 for details). Thus, the flight initiation distance data collected during 2017/18 (in (2)) was used to quantify the displacement tolerance for all individuals used in this study.

The notion of an observer approaching a habituated primate may be considered atypical or likely to result in habituation/sensitization effects or agonistic behaviours being directed towards the approaching observers. However, our previous study (see (2)) showed that almost all approaches resulted in the animal passively relocating (98.85%), a very benign response identical to the behaviours of subordinate baboons displacing away from dominant conspecifics. This suggests that in this group, observers may be considered equivalent to a high-level social threat (2). Throughout observation periods on habituated animals, observers are likely to approach or displace animals either incidentally or accidentally multiple times throughout the day, especially during lengthy focal observations. As such, the approach methodology is unlikely to represent a stimulus outside of the norm for our study animals. This may explain why displacement responses were so passive and why there was no evidence of habituation or sensitization effects across the group or individually through a range of temporal periods (see (2)). As a result, our situation was possible without risk of causing stress or anxiety in the study subjects, eliciting agonistic behaviours towards observers, or interfering with their prior habituation levels.

Statistical analysis

Quantifying displacement tolerance

FID was previously found to be distinct amongst individuals and repeatable within each individual, evidence that displacement tolerance may be an individual level trait (2). As mentioned, there was no evidence of habituation or sensitization effects within individuals or across the group, with responses consistent regardless of whether the approaching observer was familiar or unfamiliar to the study animals. Nevertheless, to further guard against these factors in this study, the model used to calculate displacement tolerance estimates (i.e., conditional modes) was updated from (2) to include additional fixed effects that tracked trial number across different levels (individual trial number per day and group trial number across all individuals per day). We also retained the observer identity and observer trial number interaction as both fixed effects and random slopes over individual identity, to ensure habituation and sensitization effects were explored effectively across all temporal levels. We removed the fixed effects of neighbour flee first and external factors within 5 minutes from the models used in (2) as they were previously shown not to effect FID in a significant way and we did not want to over parameterize the updated model.

As with (2), we also retained the fixed effects of engaged (behaviour), habitat (open/closed), height (ground/above ground), and number of neighbours within 5 meters as these were shown to be important previously. Date was also included as a random effect crossed with individual identity. Visual orientation distance index (difference between visual orientation distance and FID) was included as a fixed effect and random slope over individual identity to control for issues relating to the envelope constraint see (21, 22). In all cases, random slopes were modelled with correlated intercepts to ensure the estimated model captured all levels of by-individual variation. As this study was also focused on social factors inherent to each study animal, we also included dominance rank and age-sex class as fixed effects in the updated model, ensuring these elements of phenotypic variation were accounted for in the individual tolerance estimates. Rank was calculated using the *isi13* function from the *compete* package (23), based on all displacement, supplant, and agonistic dyadic events between April 2017 and April 2018 (n=908); fights between males were excluded as the 'winner' can often be subjective during conflict. Age-sex class was defined according to secondary sexual characteristics (e.g., testes descending/enlarging, sexual swelling, canine eruption) and changes in pelage throughout juvenile development (see supporting information text S2 for full descriptions).

The updated model was fit using the *brm* function from the *brms* package (24) in the R software (25). Each model was run for six Hamiltonian Markov chains for 15000 iterations, with warmup iterations set to 5000 and adapt_delta to 0.95. All these parameters were set higher than default to allow algorithms to converge efficiently, producing robust posterior samples (24, 26). The model was fit with a Log-normal response distribution and default link function. The Gelman-Rubin convergence diagnostic (Rhat) was equal to 1 in all cases, strongly suggesting accuracy of the response variable to the Log-normal response distribution, i.e., the standard deviation of occurrence points formed around the Log-normal function was minimal. Normal priors (mean = 0, standard deviation = 100) were assigned for all population-level effects within the brm function; the remaining model parameters were assigned default Student-*t* priors (df = 3, mean = 0, scale factor = 10), however, the standard deviations of group-level effects were constrained to be positive and therefore assigned a half Student-t prior.

We then extracted the individual conditional modes from the updated model using the *ranef* function in *brms* and performed a Pearson's correlation between the conditional modes from the updated model and the conditional modes from the previous article. Individual tolerance estimates were consistent (r(67) = .887, p < .001) despite the changes in model structure from (2). The intraclass correlation coefficient also remained almost identical (updated individual identity ICC: 0.64; highest density intervals (HDI) for posterior samples at 95% intervals, 0.53, 0.75) to the findings reported in (2) (ICC, 0.65; HDI, 0.56,0.74). We therefore used the conditional modes of each individual baboon from the updated FID model as our individual estimates for tolerance in this study.

Influence of tolerance and observer distance on inter-individual association patterns

The inter-individual association data were coded as a count of how often each individual occurred as a neighbour during the focal observations of the remaining (n-1) group members. Each individual had separate counts for each observer distance (i.e., over/under 4.5m) within each proximity buffer (i.e., touch, 1 meter, 2.5 meters, and 5 meters), separately for each year (i.e., 2018 and 2019). These counts were the response variables in four generalised linear mixed effects models (separate models for each proximity buffer). In all models, the count of occurrences was predicted by the interaction between observer distance, individual tolerance estimate, and year. Tolerance was on the spectrum whereby low/negative values indicated low tolerance and high (positive) values indicated high tolerance. We specified that all combinations of the fixed effects and their two-way interactions were also modelled.

For all models we specified the interaction between tolerance and observer distance as a random slope over individual identity, with correlated intercepts. As with the fixed effects, we also allowed the interaction to model each covariate within the interaction as separate slopes over individual identity too, whilst year was also included as a separate random slope over individual identity. All models were fit with a Bayesian procedure using the *brm* function (24) in the R software (25). Each model was run for six Hamiltonian Markov chains for 10000 iterations, warmup iterations were set to 4000 and adapt_delta to 0.99. All these parameters were set higher than default. A Poisson response distribution was defined, with default link functions, as our response variable was a count in all models. The Rhat was equal to 1 in all cases, strongly suggesting accuracy of the response variable to the Poisson response distribution; however, this was additionally validated using Cullen and Frey plots (descdist function) and posterior predictive checks via visualisation (brms and bayesplot). We used the default Student-*t* priors (df = 3, mean = 0, scale factor = 10) specified within brms for all model components, however, it should be noted these parameters are restricted to be non-negative on the standard deviations of the group-level (i.e., random effects), thus a half Student-t prior was implemented for these parameters. Using the pp_check function (brms and bayesplot) we simulated values of the posterior predictive distribution for each model and compared them to the observed data to confirm accurate and reliable estimates were produced that were not biased by our choice of priors or response distributions (24).

Relying purely on model estimates and 95% credible intervals for inference can be subjective and overlooks the extent to which the posterior is equivalent to zero (27). Therefore, to ensure as much information about the posterior was included in inference, we additionally calculated the 89% Highest Density Interval (HDI) of the posterior distribution, the percentage of the posterior distribution within the region of practical equivalence (ROPE), and the probability of direction (pd) for each population-level (i.e., fixed) effect within each model. The HDI reveals the upper and lower parameter values of the posterior based on all values within the 89% range, these points therefore have a higher probability density than those outside the 89% range (28). The ROPE is the region that equates to the null hypothesis, although there are no set rules for defining this interval as it relates to the variables being analysed (see (28)). In our case the response variable was a count and so we defined the area around 0 that equated to the ‘null’ as -0.1 to 0.1, and this was additionally validated using the *rope_range* function from *bayestestR* (29). We therefore computed the proportion of the 89% HDI of the posterior distribution within the -0.1 to 0.1 ROPE range. The pd variable is an index for inspecting whether each fixed effect has directionality (i.e., is positive or negative); pd always ranges from a minimum of 50% (i.e., equal distribution of positive and negative posterior values) to 100% (i.e., all posterior values are either positive or negative) (30). It has been shown that pd has a 1:1 correspondence with p-values calculated using frequentist methods (30)

Results

Flight initiation distance model

We found no evidence that the study subjects habituated or sensitized across any timeframe to the approaches completed previously (see supporting information table S1). Ongoing monitoring of study subject’s behavioural responses also validated this (see (2)), providing strong evidence that the methods did not create stress or anxiety in the study subjects. We also found no evidence that dominance rank was a driver of FID (estimate 0 lower and upper credible intervals: -0.01, 0). Adult females with and without infants, and adult males seem to generally exhibit slightly longer FIDs than younger individuals (see table S1), although the credible intervals overlapped with other age-sex classes. The other age-sex classes produced generally similar FIDs with wide credible intervals overlapping with one another (see fig 1). However, there was a general trend for FIDs to increase with age-sex class category in male individuals (i.e., mean conditional effect of FID in adult males > juvenile-3 males > J2M > J1M). This was not the case in female individuals as the mean conditional effect of FID was higher for all juvenile females than adolescent females.

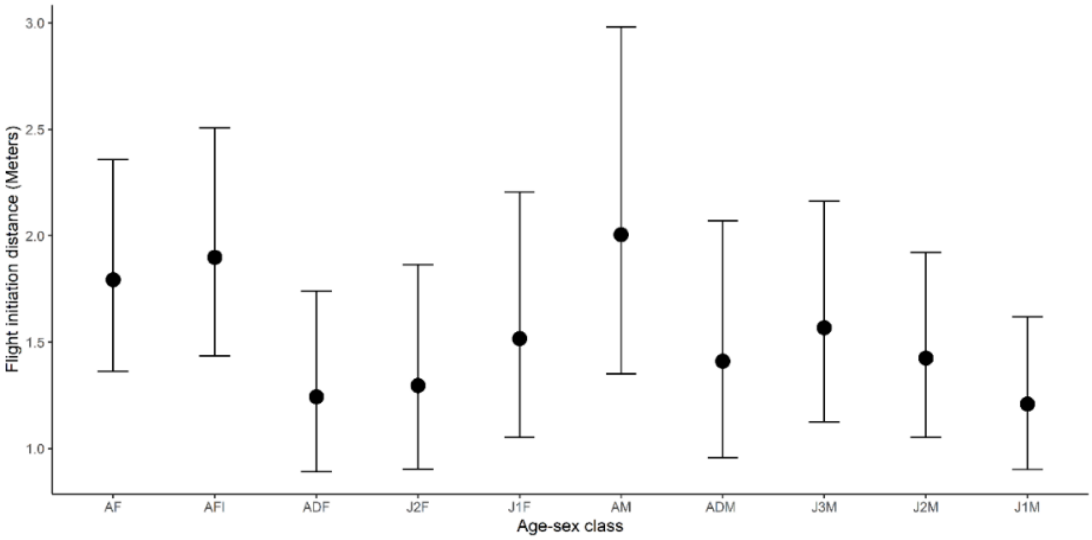

Fig 1. Conditional effects plot for each age-sex class and flight initiation distance. The mean was used as the measure of central tendency, 2.5 and 97.5% percent credible intervals also displayed. From left to right on the x-axis: adult females without infants (AF), adult females with infant (AFI), adolescent females (ADF), juvenile-2 females (J2F), juvenile-1 females (J1F), adult males (AM), adolescent males (ADM), juvenile-3 males (J3M), juvenile-2 males (J2M), and juvenile-1 males (J1M) (see text S2 for descriptions).

Inter-individual association patterns

The population-level effects calculated from the mixed model analysis (see table 1) suggest strong evidence that the 3-way interaction between tolerance, observer distance, and year influenced the population-level mean for occurrences as a neighbour. Conditional effects plots (see fig 2) display the predicted population-level means for number of occurrences as a neighbour conditioned on the interaction between tolerance and observer distance, for each year; highlighting a consistent (across years and proximity buffers) positive relationship (when the observer was at less than 4.5 meters) between tolerance and the population-level mean for occurrences as a neighbour. Interestingly, this effect is neutralised when data is collected from over 4.5 meters, i.e., the population-level mean remained relatively constant across the tolerance spectrum.

Table 1. Model summary results for population-level effects for all four models, columns represent the data recorded from each proximity buffer. Each cell represents the model estimates with the upper and lower 89% highest density intervals (HDI) in parenthesis, bold cells highlight where HDI

	5 meter buffer	2.5 meter buffer	1 meter buffer	Touch buffer
Intercept	**2.99 (2.91, 3.08)**	**2.11 (2, 2.23)**	**1.31 (1.18, 1.44)**	**0.52 (0.35, 0.71)**
Tolerance	0 (-0.23, 0.25)	0.03 (-0.29, 0.34)	0.13 (-0.21, 0.47)	0.1 (-0.36, 0.53)
Observer Distance (Under 4.5m)	**0.37 (0.29, 0.44)**	**0.34 (0.23, 0.46)**	0.16 (-0.03, 0.35)	-0.11 (-0.38, 0.15)
Year (2019)	0.06 (-0.02, 0.13)	**0.28 (0.18, 0.39)**	**0.32 (0.18, 0.46)**	**0.53 (0.34, 0.72)**
Tolerance : Observer Distance (Under 4.5m)	**0.3 (0.06, 0.54)**	0.33 (0, 0.66)†	0.4 (-0.13, 0.94)	**0.7 (0.02, 1.36)***
Tolerance : Year (2019)	-0.07 (-0.27, 0.12)	-0.1 (-0.37, 0.17)	-0.08 (-0.43, 0.27)	-0.07 (-0.51, 0.39)
Observer Distance (Under 4.5m) : Year (2019)	**-0.17 (-0.25, -0.09)**	**-0.28 (-0.4, -0.16)**	**-0.43 (-0.62, -0.23)**	**-0.4 (-0.7, -0.11)**
Tolerance : Observer Distance (Under 4.5m) : Year (2019)	**0.31 (0.08, 0.52)**	**0.51 (0.19, 0.85)**	**0.75 (0.24, 1.26)**	0.54 (-0.16, 1.27)

parameter values did not include zero. Orange cells highlight when less than 2.5% of the 89% HDI fell within the -0.1 to 0.1 range (ROPE) and the probability of direction was greater than 97.5%, which indicates very strong evidence that the most credible parameter values derived from each model are outside of the area equivalent to the null with high certainty of effect existence (i.e, positive/negative direction). Green cells highlight where between 2.5% and 5% were within the ROPE and pd was greater than 97.5%. *pd = 95%. ⁺ROPE = 8% and pd = 95%.

Figure 2 also highlights that the point where the mean conditional effects for each observer distance (over/under 4.5m) intersects shifts right along the horizontal axis (towards more tolerant animals) as the proximity buffer is narrowed. For example, for the 5m and 2.5m proximity buffers for 2018, the conditional mean when the observer was under 4.5m was greater than the upper 95% credible interval for when the observer was over 4.5m for most of the tolerance spectrum. However, the mean conditional effects of observer distance converge as tolerance decreases, suggesting tolerant animals were oversampled when the observer was under 4.5m for the 5m and 2.5m proximity buffers in 2018.

Within the narrower proximity buffers of 1 meter or touch, the intersection of mean conditional effects occurs further along the tolerance spectrum, suggesting numerous individuals were under sampled when the observer was close, i.e., the mean conditional effect for under 4.5m was lower than the lower 95% credible interval of over 4.5m for these parts of the tolerance spectrum. In all cases the mean conditional effect for under 4.5m was higher than the upper 95% credible interval of over 4.5m at the highest portion (right-side) of the tolerance spectrum. In summary, across both years and all proximity buffers tolerance shared a positive relationship with how often animals occurred as neighbours when the observer was close, but tolerance and occurrences shared a neutral relationship when the observer was further away.

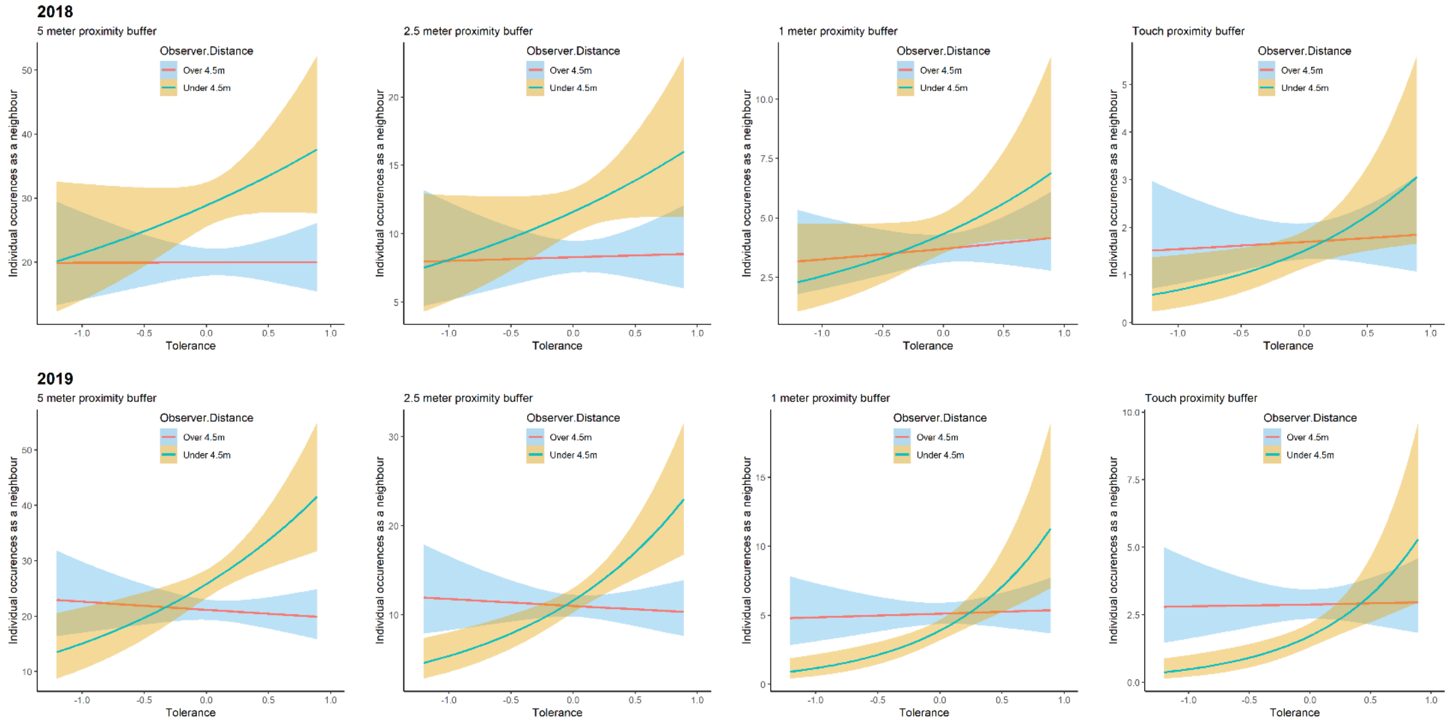

Fig 2. Conditional effects plots of model results predicting the effect of the interaction between individual displacement tolerance (high values indicate highly tolerant animals) and observer distance on the number of occurrences each individual has as a neighbour for the remaining group members for 2018 and 2019. The mean was used as the central tendency, with the shaded areas displaying the relevant credible intervals (2.5 and 97.5 percent quantiles).

As population-level parameters are modelled as identical for all individuals, the group-level (or varying) effects of each model also display important information at the individual-level (see table 2). In general, the among-individual standard deviations were very close to the magnitude of the population-level effects shown in table 1, suggesting individual identity was an important component governing the number of occurrences as a neighbour. There was no consistent evidence that slopes varied according to year, observer distance, or individual tolerance level (see table 2: cor estimates); however, specific insights into individual-level effects (see fig 3) highlight that numerous trends underly these results.

Table 2. Model summary results for individual-level effects for all four models, columns represent the data recorded from each proximity buffer. Each cell represents the model estimates with the upper and lower 89% highest density intervals (HDI) in parenthesis, bold cells highlight where HDI parameter values did not include zero. Orange cells highlight when less than 2.5% of the 89% HDI fell within the -0.1 to 0.1 range (ROPE) and the probability of direction was greater than 97.5%. *pd = 100%, ROPE = 7.98%. †pd = 96.78%, ROPE = 0%.

	5 meter buffer	2.5 meter buffer	1 meter buffer	Touch buffer
sd(Intercept)	**0.34 (0.26, 0.42)**	**0.41 (0.3, 0.51)**	**0.33 (0.19, 0.48)**	**0.41 (0.23, 0.59)**
sd(Year2019)	**0.21 (0.14, 0.27)**	**0.25 (0.15, 0.34)**	**0.2 (0.01, 0.34)**	0.16 (0, 0.31)
sd(Tolerance)	**0.45 (0.22, 0.68)**	**0.55 (0.22, 0.87)**	0.4 (0, 0.75)	0.39 (0, 0.77)
sd(Observer Distance - Under4.5m)	**0.15 (0.05, 0.26)**	**0.27 (0.11, 0.41)**	**0.48 (0.27, 0.69)**	**0.61 (0.36, 0.86)**
sd(Tolerance : Obs.Dist - Under4.5m)	**0.62 (0.38, 0.86)**	**0.58 (0.08, 0.98)**	**1.07 (0.35, 1.74)**	0.71 (0, 1.3)*
cor(Intercept,Year2019)	**-0.73 (-0.92, -0.55)**	**-0.74 (-0.95, -0.53)**	**-0.18 (-0.74, 0.39)**	**-0.12 (-0.76, 0.49)**
cor(Intercept,Tolerance)	**-0.51 (-0.85, -0.17)**	**-0.4 (-0.8, -0.03)**	-0.15 (-0.73, 0.41)	-0.1 (-0.72, 0.49)
cor(Year2019,Tolerance)	0.31 (-0.13, 0.78)	**0.45 (0.06, 0.9)**	0 (-0.63, 0.64)	0.02 (-0.61, 0.67)
cor(Intercept,Obs.Dist - Under4.5m)	0.07 (-0.39, 0.51)	-0.29 (-0.68, 0.07)	**-0.43 (-0.83, -0.07)**†	**-0.52 (-0.87, -0.2)**
cor(Year2019,Obs.Dist - Under4.5m)	-0.25 (-0.73, 0.18)	-0.01 (-0.47, 0.46)	-0.27 (-0.82, 0.23)	0.04 (-0.59, 0.66)
cor(Tolerance,Obs.Dist - Under4.5m)	-0.1 (-0.68, 0.47)	-0.05 (-0.62, 0.51)	0.12 (-0.46, 0.74)	0.21 (-0.37, 0.85)
cor(Intercept,Tolerance : Obs.Dist - Under4.5m)	0 (-0.42, 0.40)	0.05 (-0.46, 0.62)	0.31 (-0.17, 0.81)	0.3 (-0.24, 0.9)
cor(Year2019,Tolerance : Obs.Dist - Under4.5m)	-0.1 (-0.52, 0.30)	-0.1 (-0.64, 0.44)	-0.01 (-0.62, 0.59)	-0.02 (-0.67, 0.63)
cor(Tolerance,Tolerance : Obs.Dist - Under4.5m)	0.1 (-0.38, 0.58)	-0.08 (-0.64, 0.5)	-0.04 (-0.63, 0.58)	-0.18 (-0.84, 0.44)
cor(Obs.Dist - Under4.5m,Tolerance : Obs.Dist - Under4.5m)	-0.36 (-0.81, 0.05)	-0.22 (-0.71, 0.29)	-0.4 (-0.83, 0.01)	-0.29 (-0.87, 0.25)

For the most part, all but very intolerant individuals seem to be observed more frequently (i.e., over-sampled) when the observer was within 4.5m for the 5m proximity buffer (see fig 3). Very intolerant animals were the only animals to consistently occur less frequently (i.e., under-sampled) when the observer was within 4.5m relative to over 4.5m, this effect amplified as the proximity buffer narrowed. Within the remaining tolerance bins (i.e., low, medium, high, very high tolerance) individuals produced varying responses to observer distance within the 2.5m and 1m proximity buffers, however there was a general trend for individuals to occur less frequently when the observer was within 4.5m as the proximity buffer narrowed. For example, 'medium' tolerance individuals generally occurred more frequently (i.e., over-sampled) when the observer was within 4.5m for the 5m and 2.5m proximity buffer, but several individuals reversed this trend for the 1m buffer, with most occurring far less frequently (i.e., under-sampled) in the touch buffer when the observer was closer. Almost all individuals displayed a negative slope for observer distance for the touch models, i.e., they occurred less frequently when the observer was close, suggesting strong evidence that touch associations were under-sampled for the majority of individuals when the observer was within 4.5m.

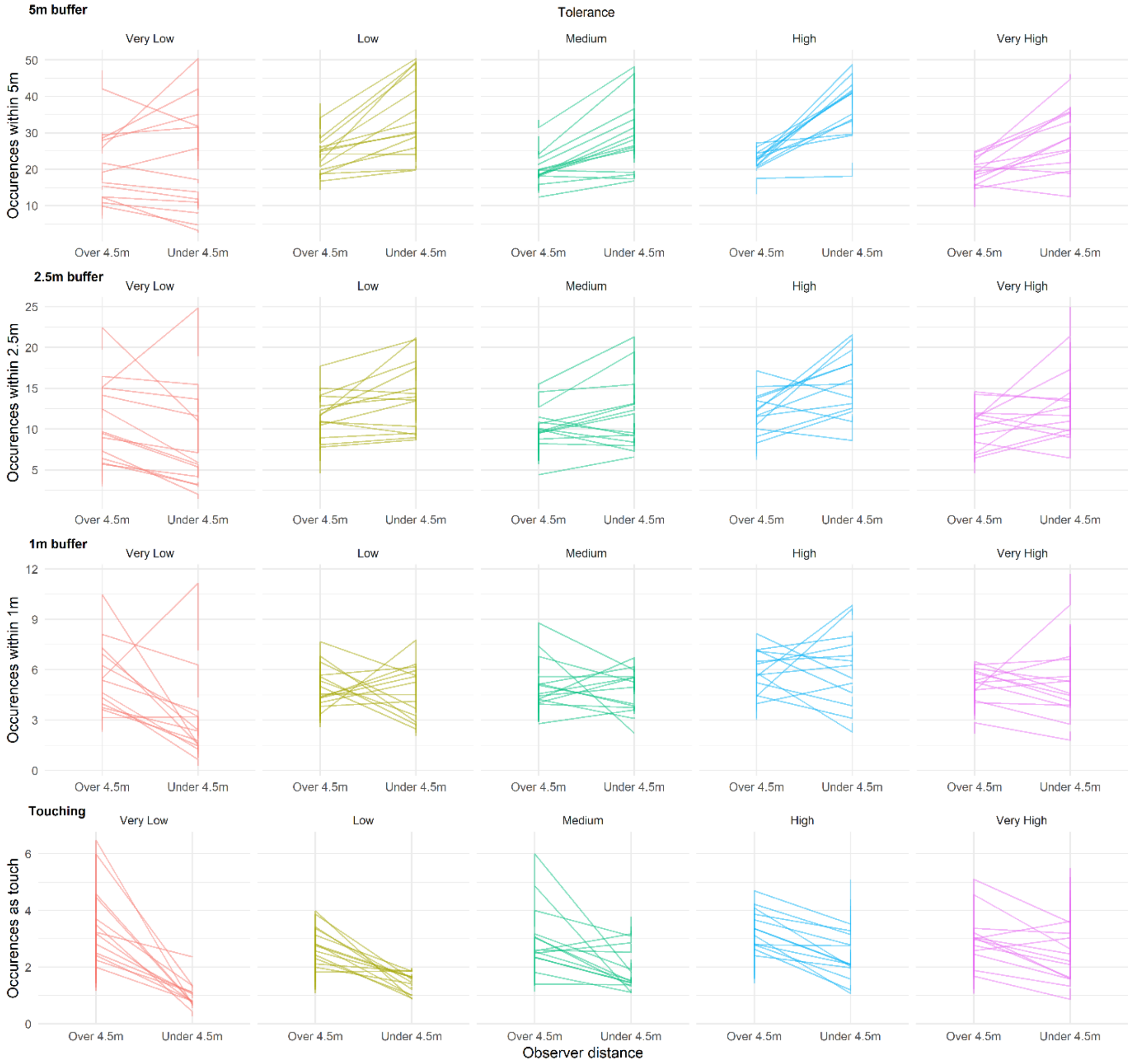

Fig 3. Line graphs representing the predicted individual-level means for occurrences as a neighbour at each observer distance across years. Each row represents the independent proximity buffer models. Within each row tolerance is separated into five equal bins of very low, low, medium, high, and very high.

Discussion

We tested whether the interaction between tolerance and observer distance influenced how often other individuals were observed in proximity to focal animals. At the population-level, there was clear evidence that when the observer was closer (i.e., under 4.5m) there was a positive association between tolerance and the number of times an individual occurred as a neighbour to focal animals. Group-level results highlighted that many individuals appeared to be oversampled (relative to the mean) in the 5m and 2.5m buffers when the observer was close, including some individuals slightly lower on the tolerance spectrum. As the proximity buffers narrowed (i.e., 1m and touch), few individuals appeared to remain oversampled, whilst many animals (not only intolerant individuals) were under sampled. The population-level results highlighted that when the observer was further away (i.e., over 4.5m) there was generally a neutral relationship between tolerance and occurrences, across both years and all proximity buffers. These results suggest that inter-individual associations would be challenging to sample without bias in this study group unless observation distances were kept above a certain threshold.

Our results suggest that most of our study group were highly habituated and that ‘low’ relative tolerance (within the study group) may still be indicative of being fairly tolerant of observers. For example, several individuals who had ‘low’ tolerance still occurred more frequently in the 5m and 2.5m buffers when the observer was within 4.5m. The finding that numerous animals were oversampled in the larger proximity buffers (i.e., 2.5 and 5m) when focals were completed at less than 4.5 meters may suggest that tolerant phenotypes could be favouring areas near observers. An awareness of tolerance differences could aid subordinate animals in accessing food patches or avoiding aggressions from dominant animals who are less tolerant. Although we found no evidence that dominance rank influenced FID in this study, this does not test whether tolerant animals can exploit a tolerance-derived phenotypic advantage during agonistic or competitive scenarios. This poses an interesting question for future work, in asking whether habituated animals are aware of the tolerance differential between them and use this differential to their advantage.

To our knowledge, this is the first study to demonstrate that highly habituated animals will assort themselves according to tolerance phenotype and observer behaviour. Previous work has highlighted that not all measures of inter-individual association patterns measure the same information, leading to fundamentally different networks (14); our results suggest observer distance could be just as important methodological information as the parameters used to measure associations. In addition, these results could also explain some of the differences between networks as close proximity or association (e.g., affiliative or grooming interactions) measures may be more susceptible to bias than longer distance rules. Undertaking observations from further away and focusing on larger proximity buffers (e.g., 5 meters) may reduce this effect on intolerant animals. Field sites dominated by open habitats may be best placed to do both; undoubtedly, many researchers do this already. However, the specific distances may need testing in each study system and field site, especially where challenging terrain and dense vegetation may limit the practicality of wider proximity buffers and longer observation distances.

The outcome of habituation processes are often classified in qualitative terms, e.g., ‘full habituation’ (31), and such terms have been used even when inter-individual differences in observer tolerance remain, e.g., (9). The baboons used in this study received observations for nearly a decade and so had been habituated to researchers over a long period (17, 18). This strongly suggests our group would be considered ‘fully habituated’, and yet consistent inter-individual differences in tolerance remained (2). Study animals receiving short term or sporadic study attention, or earlier in the habituation process, are unlikely exhibit similarly high tolerance levels; as a result, observer presence and behaviour are likely to have greater impact. In our case, as AA was the main observer over a 4.5-year period (over 400 full-day observations) and completed all focal observations used in this study, inter-observer effects were not considered. However, field sites with regular turn-over in researchers may need to consider whether the interaction between observer distance/behaviour and individual tolerance estimates is consistent across observers as well. Given the complexities of habituation and tolerance, and the variation that likely exists between individuals, groups, populations, and species, it seems important that future research using direct observations on habituated animals routinely measures tolerance levels and communicates the outcomes as vital elements of methodological information going forward.

Collecting data on intolerant animals has always been a challenging task, with some researchers electing to exclude them entirely (e.g., (33)), however, this strategy does not remove the probability of intolerant animals occurring as neighbours for the remaining (n-1) group members. Excluding individuals based on age classifications (e.g., juveniles) has been shown to create fundamentally different networks (33); therefore removing individuals based on phenotype will likely introduce a level of bias into networks. Recently, social network research has explored ways of dealing with missing data (see (34, 35), but when missing data is produced from a non-random process it affects a range of networks and metrics in different ways leading to biased outcomes (36). In this case, the interaction between tolerance and observer distance appears to be an overlooked ecological driver of inter-individual association patterns in these habituated animals and not a random process. As such, solutions must focus on avoiding sampling bias in situ instead of relying on analytical solutions post-hoc. One option is to explore methods of gathering data without human-presence, with GPS (or radio) collars and camera-trapping potential solutions (37). Aside from the ethical concerns associated with collaring (38), there are challenges fitting GPS collars to all individuals and numerous reliability issues (e.g., (39)) which means it is unlikely to offer an immediate solution to the problem of excluding groups of individuals and missing data (e.g., (33, 36)). Similarly, many individuals may be challenging to capture on camera-traps or other automated technologies.

The use of FID methodology has been rare in primatology thus far, and so it is unclear if such methods are viable elsewhere. Future work should only utilise approach methodology if similarly, benign responses are expected across all study subjects initially and throughout all stages of data collection. Tangential approaches and measuring visual orientation/detection (instead of flight/displacement) may be a more viable option if researchers only need to ascertain appropriate observation distances, although tangential approaches may not elicit responses in very tolerant animals. Nevertheless, measuring visual orientation distance using tangential approaches would offer researchers a less demanding method for tracking individual tolerance levels routinely and could be used to understand the differences in habituation and tolerance that may be present across different field sites, species, and individuals through time, although there would need to be consolidation on defining visual orientation for this to be feasible (40). Future research should also explore ways of investigating habituation, sensitization, and tolerance effects in habituated animals without the use of approach methodology as it is unlikely to be viable in scenarios where animals have become ‘over-habituated’ or aggressive towards humans already. It would be useful to explore why these tendencies have emerged at certain locations and its impact on the data collected, as it again would suggest researchers are no longer a neutral stimulus (2).

Although observer presence may be considered a low level of anthropogenic disturbance, it can have differential impacts on habituated and non-habituated animals (41). Non-focal animals, particularly predators, are often displaced by human-activities (42), resulting in increased energetic costs (43) and potential disruption to vital ecological processes such as predation and competition for resources (37). Despite our study focusing on habituated animals, we still found that the presence and behaviour (i.e., distance) of observers led to phenotypic assortment. These results demonstrate that overlooking observer factors and tolerance may impact on the quality of data collected, suggesting that future studies need to carefully consider the impacts of observer presence on both focal and non-focal animals.

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References

1. K. T. Hanson, E. P. Riley, Beyond Neutrality: the Human–Primate Interface During the Habituation Process. *Int. J. Primatol.* **39**, 852–877 (2017).
2. A. T. L. Allan, A. L. Bailey, R. A. Hill, Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Sci. Adv.* **6**, eaaz0870 (2020).
3. B. B. Smuts, *Sex and Friendship in Baboons* (Harvard University Press, 1999).
4. L. Alcayna-stevens, Habituating field scientists. *Soc. Stud. Sci.*, 1–21 (2016).
5. M. Candea, Habituating Meerkats and Redescribing Animal Behaviour Science. In J. Latimer & M. Miele (Eds.), Naturecultures: Science, Affect and the Non-human. *Theory Cult. Soc.* **30**, 105–129 (2013).
6. R. J. Welch, A. le Roux, M. B. Petelle, S. Périquet, The influence of environmental and social factors on high- and low-cost vigilance in bat-eared foxes. *Behav. Ecol. Sociobiol.* **72**, 1–10 (2018).
7. B. M. Titus, M. Daly, D. A. Exton, Do Reef Fish Habituate to Diver Presence? Evidence from Two Reef Sites with Contrasting Historical Levels of SCUBA Intensity in the Bay Islands , Honduras. *PLoS One* **10**, e0119645 (2015).
8. H. Whitehead, Analysing animal social structure. *Anim. Behav.* **53**, 1053–1067 (1997).
9. Q. M. R. Webber, E. Vander Wal, Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.* **149**, 77–87 (2019).
10. T. Wey, D. T. Blumstein, W. Shen, F. Jordán, Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344 (2008).
11. N. Pinter-Wollman, *et al.*, The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255 (2014).
12. K. S. Morrow, H. Glanz, P. O. Ngakan, E. P. Riley, Interactions with humans are jointly influenced by life history stage and social network factors and reduce group cohesion in moor macaques (*Macaca maura*). *Sci. Rep.* **9**, 1–12 (2019).
13. V. M. Green, K. I. Gabriel, Researchers' ethical concerns regarding habituating wild-nonhuman primates and perceived ethical duties to their subjects: Results of an online survey. *Am. J. Primatol.* **82**, e23178 (2020).
14. M. Castles, *et al.*, Social networks created with different techniques are not comparable. *Anim. Behav.* **96**, 59–67 (2014).
15. S. P. Henzi, D. Lusseau, T. Weingrill, C. P. Van Schaik, L. Barrett, Cyclicity in the structure of female baboon social networks. *Behav. Ecol. Sociobiol.* **63**, 1015–1021 (2009).
16. A. J. King, F. E. Clark, G. Cowlishaw, The dining etiquette of desert baboons: The roles of social

bonds, kinship, and dominance in co-feeding networks. *Am. J. Primatol.* **73**, 768–774 (2011).

17. A. L. de Raad, R. A. Hill, Topological spatial representation in wild chacma baboons (*Papio ursinus*). *Anim. Cogn.* **22**, 397–412 (2019).

18. C. Howlett, J. M. Setchell, R. A. Hill, R. A. Barton, The 2D : 4D digit ratio and social behaviour in wild female chacma baboons (*Papio ursinus*) in relation to dominance, aggression, interest in infants, affiliation and heritability. *Behav. Ecol. Sociobiol.* **69**, 61–74 (2015).

19. A. T. L. Allan, R. A. Hill, A. L. Bailey, Flight and visual orientation distance remained consistent in a single group of habituated chacma baboons after an observed predation by a leopard. Do flight initiation distance methods always measure perceived predation risk?. *Rev.*

20. D. T. Blumstein, D. S. M. Samia, T. Stankowich, W. E. Cooper, "Best practice for the study of escape behavior" in *Escaping from Predators: An Integrative View of Escape Decisions*, W. E. Cooper, D. T. Blumstein, Eds. (Cambridge University Press, 2015), pp. 405–419.

21. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).

22. N. C. Bonnot, *et al.*, Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).

23. J. P. Curley, compete: Analyzing Social Hierarchies: R package version 0.1 (2016).

24. P.-C. Bürkner, brms : An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

25. R Core Team, R: A language and environment for statistical computing. Version 3.6.1. *R Found. Stat. Comput. Vienna, Austria* (2019).

26. R. McElreath, *Statistical Rethinking 2: A Bayesian Course with Examples in R and Stan*, Second (2019).

27. J. K. Kruschke, Rejecting or Accepting Parameter Values in Bayesian Estimation. *Adv. Methods Pract. Psychol. Sci.*, 1–11 (2018).

28. J. K. Kruschke, T. M. Liddell, Bayesian data analysis for newcomers. *Psychon. Bull. Rev.* **25**, 155–177 (2018).

29. D. Makowski, M. S. Ben-Shachar, D. Lüdecke, bayestestR : Describing Effects and their Uncertainty , Existence and Significance within the Bayesian Framework. *J. Open Source Softw.* **4(40)**, 1–8 (2019).

30. D. Makowski, M. S. Ben-Shachar, S. H. A. Chen, D. Ludecke, Indices of Effect Existence and Significance in the Bayesian Framework. *Retrieved from https//doi.org/10.31234/osf.io/2zex*, 1–35 (2019).

31. P. Bertolani, C. Boesch, Habituation of wild chimpanzees (*Pan troglodytes*) of the south group at Taï Forest, Côte d'Ivoire: Empirical measure of progress. *Folia Primatol.* **79**, 162–171 (2008).

32. E. Gazagne, A. Hambuckers, T. Savini, P. Poncin, M. Huynen, Toward a better understanding of habituation process to human observer: A statistical approach in Macaca leonina (Primates: *Cercopithecidea*). *Raffles Bull. Zool.* **68**, 735–749 (2020).

33. P. Fedurek, J. Lehmann, The effect of excluding juveniles on apparent adult olive baboons (*Papio anubis*) social networks. *PLoS One* **12**, e0173146 (2017).

34. W. J. E. Hoppitt, D. R. Farine, Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* **136**, 227–238 (2018).

35. M. J. Silk, A. L. Jackson, D. P. Croft, K. Colhoun, S. Bearhop, The consequences of unidentifiable individuals for the analysis of an animal social network. *Anim. Behav.* **104**, 1–11 (2015).

36. J. A. Smith, J. Moody, J. H. Morgan, Network sampling coverage II: The effect of non-random missing data on network measurement. *Soc. Networks* **48**, 78–99 (2017).

37. L. R. LaBarge, R. A. Hill, C. M. Berman, S. W. Margulis, A. T. L. Allan, Anthropogenic influences on primate antipredator behavior and implications for research and conservation. *Am. J. Primatol.* **82**, e23087 (2020).

38. M. S. McCarthy, *et al.*, Camera traps provide a robust alternative to direct observations for constructing social networks of wild chimpanzees. *Anim. Behav.* **157**, 227–238 (2019).

39. G. H. Davis, M. C. Crofoot, D. R. Farine, Estimating the robustness and uncertainty of animal social networks using different observational methods. *Anim. Behav.* **141**, 29–44 (2018).

40. A. T. L. Allan, R. A. Hill, Definition and interpretation effects: How different vigilance definitions can produce varied results. *Rev.*

41. A. P. Møller, Urban areas as refuges from predators and flight distance of prey. *Behav. Ecol.* **23**, 1030–1035 (2012).

42. T. B. Muhly, C. Semeniuk, A. Massolo, L. Hickman, M. Musiani, Human activity helps prey win the predator-prey space race. *PLoS One* **6**, e17050 (2011).

43. Y. Wang, J. A. Smith, C. C. Wilmers, Residential development alters behavior, movement, and energetics in a top carnivore. *PlosOne* **12**, e0184687 (2017).

Supporting information

Text S1. Testing consistency of tolerance across years

To understand whether tolerance estimates varied between years we repeated the procedures outlined in (1) on a subset of 15 individuals (approximately 25% of group members) that were present across 2017, 2018, and 2019. Due to time constraints and results from the previous approach we allowed for up to 4 approaches per individual per sample day, but never sequentially. All individuals received 12 approaches by AA for the 2019 samples.

For the first part of this analysis, we combined the data collected during 2017 and 2018 with the data collected during 2019. The analysis described in (1) was repeated on this dataset. The only changes to this FID model were the removal of the observer identity and its interaction with trial number (per observer) as only AA completed trials in 2019 (observer identity had little effect on FID previously). Individual trial number per observer was included as a fixed effect and random slope over individual identity, trial number restarted from 1 for AA's additional trials in 2019 given the previous trials had taken place more than 12 months previously. Group trial number per day and individual trial number per day were also included as fixed effects to control for habituation and sensitization effects across a number of temporal levels. We also included 'year' as a fixed effect to explore consistency between years across all individuals. We removed the fixed effects of neighbour flee first and external factors within 5 minutes from the models used in (1) as they were previously shown not to effect FID in a significant way and we did not want to over parameterize the model. With 2017 as the reference category, the model estimates for 2018 and 2019 were 0.11 (-0.06,0.28) and 0.05 (-0.11,0.22) respectively. In each case estimates were close to zero with credible intervals overlapping zero, providing strong support for there being no effect of year on FID.

In addition, we ran a 2019 model using the same analytical framework as described above based only on 2019 FID data from the sample of 15 individuals. The only changes to the model was the removal of the covariate 'year'. We then extracted the individual conditional modes from the model and performed a Pearson's correlation between the 2019 conditional modes and the conditional modes from the updated model (from the main text - 2017/18 data). Results supported that tolerance estimates were consistent across years (r(13) = .905, p < .001), as such we felt confident utilising the data collected during 2017/2018 for all individuals in the updated. Conditional modes extracted from the previous study (see (1)) were originally on the spectrum whereby highly tolerant animals had low/negative estimates and highly intolerant animals had high/positive estimates; therefore, tolerance was multiplied by minus 1 to reverse the scale for more logical inference in this study.

Text S2. Age-sex class categories and descriptions

Female baboons:

AF (Adult female) – Attainment of full body size, either cycling regularly, pregnant or lactating. Nipples also enlarge and elongated from suckling infants.

AFI (Adult female with infant) – As above but with their own neonate or dependent infant. Approaches were not completed on individuals known to have dependent infants but when those infants were not attached (e.g., suckling, being carried dorsally or ventrally) to the mother.

ADF (Adolescent Female) – Nearly adult female size, with the onset of the first sexual swellings. If visible, nipples are much smaller and button-like than that of an adult female.

Male baboons:

AM (Adult male) – All secondary sexual characteristics fully grown, musculature (most noticeably in chest and rump) expands to full adult size.

ADM (Adolescent Male) – Massive growth in secondary sexual characteristics; testes expand, canines and mane grow longer, body size increases to near that of an adult male.

J3M (Juvenile 3 Males Only) – Body size that of an adult female, muzzle further extended to nearly that of an adult male. Testes start to expand and are clearly visible. Mane becomes noticeable.

Juvenile baboons of both sexes:

J2M/F (Juvenile 2) – Little demarcation from previous period, with greater body size. Hair becomes darker, changing to a more adult grey/brown colouration.

J1M/F (Juvenile 1) – Little demarcation from infants, but fully weaned and nutritionally independent. Muzzle starts becoming more elongated and pronounced. Pelage is still lighter than in juvenile 2. Male/female distinction based on genitalia and noticeable absence/presence of a separation in the callosities.

Table S1. Updated FID model summary. Parameter estimates for the model describing the relationship between FID and the predictor variables.

Population-level effects

	Estimate	Est.Error	L-95% CI	U-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	0.53	0.28	-0.02	1.08	1.00	23080	34474
VODI	-0.04	0.01	-0.07	-0.01	1.00	62901	47626
Not engaged (Behaviour)	0.14	0.02	0.1	0.18	1.00	98751	45889
Open (Habitat)	0.12	0.02	0.08	0.17	1.00	102048	46839
Ground (Height)	0.1	0.06	-0.01	0.22	1.00	104609	46967
Number of neighours	-0.08	0.01	-0.09	-0.06	1.00	106236	48976
Unfamiliar observer (AB)	-0.08	0.17	-0.41	0.26	1.00	33784	38404
Individual trial number per observer	-0.02	0.01	-0.05	0	1.00	48298	46077
Group trial number per observation day	0	0.01	-0.01	0.01	1.00	39755	41666
Individual trial number per observation day	-0.04	0.03	-0.09	0.02	1.00	91378	46091
Dominance rank	0	0	-0.01	0	1.00	20339	30644
Adolescent males	0.13	0.23	-0.32	0.58	1.00	17683	30909
Adolescent females	0.37	0.14	0.08	0.65	1.00	20003	31773
Adult females with infants	0.42	0.14	0.14	0.7	1.00	20766	32997
Adult males	0.48	0.23	0.02	0.94	1.00	17104	27684
Juvenile females (J1F)	0.2	0.21	-0.21	0.61	1.00	19358	30125
Juvenile males (J1M)	-0.03	0.18	-0.39	0.33	1.00	15046	26180
Juvenile females (J2F)	0.04	0.21	-0.36	0.45	1.00	19238	29162
Juvenile males (J2M)	0.14	0.19	-0.23	0.5	1.00	14707	25519
Juvenile males (J3M)	0.23	0.2	-0.17	0.63	1.00	15655	27616
Unfamiliar observer (AB) : Trial number per observer	0.02	0.01	0	0.05	1.00	32055	39490

Family specific (log-normal)

Sigma	0.36	0.01	0.34	0.37	1.00	53117	44447

Group-level effects

Date (58 levels)							
sd(Intercept)	0.14	0.02	0.11	0.19	1.00	19919	34033
Individual identity (69 levels)							
sd(Intercept)	0.44	0.05	0.35	0.55	1.00	24368	35442
sd(VODI)	0.06	0.02	0.02	0.09	1.00	16349	17044
sd(ObserverAB)	0.16	0.04	0.07	0.24	1.00	21648	20637
sd(TrialNo)	0.01	0	0	0.02	1.00	16389	28088
sd(ObserverAB:TrialNo)	0.01	0.01	0	0.02	1.00	11329	20751
cor(Intercept,VODI)	0.24	0.23	-0.2	0.68	1.00	34070	32932
cor(Intercept,ObserverAB)	0.2	0.22	-0.24	0.63	1.00	34330	37639
cor(VODI,ObserverAB)	0.15	0.3	-0.43	0.7	1.00	16420	28401
cor(Intercept,TrialNo)	-0.39	0.32	-0.86	0.39	1.00	45787	41246
cor(VODI,TrialNo)	-0.13	0.36	-0.77	0.61	1.00	34154	41653
cor(ObserverAB,TrialNo)	-0.28	0.35	-0.84	0.48	1.00	38443	44739
cor(Intercept,ObserverAB:TrialNo)	-0.17	0.31	-0.73	0.48	1.00	45586	40167
cor(VODI,ObserverAB:TrialNo)	-0.4	0.33	-0.88	0.38	1.00	29482	36482

cor(ObserverAB,ObserverAB:TrialNo)	-0.05	0.36	-0.66	0.68	1.00	40037	44460
cor(TrialNo,ObserverAB:TrialNo)	-0.14	0.39	-0.79	0.66	1.00	20364	38698

Chapter 7. The key vigilance and behavioural predictors of looking in a habituated group of chacma baboons

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AA conceived and coordinated the study, collected all field data, carried out statistical analysis, and drafted the initial manuscript. AA and RH designed the study with equal contribution. RH participated in statistical analysis and critically revised the manuscript.

Abstract

Animal vigilance has been a popular research theme for several decades; however, recent research has highlighted the inherent challenges in sampling vigilance accurately, especially in wild primates. A potential solution to this issue may be to sample more general visual search behaviours such as looking, however, as many factors are likely to be associated with looking, such an approach requires many alternative hypotheses to be explored within the same analytical framework. In this study, we undertook direct observations of a habituated group of gray-footed chacma baboons (*Papio ursinus griseipes*) sampling their looking behaviours continuously whilst also recording detailed information on numerous contextual factors. We evaluated the key scenarios likely to predict changes in their looking patterns by comparing the strength of biological hypotheses in a model comparison framework. This approach weighted the competing hypotheses in unison and revealed that the study animals increased the duration of looking behaviours in response to encounters with other groups and ongoing social risk events (i.e., wahoos and within-group aggressions). Both the duration and frequency of looking bouts shared strong positive associations with the number of within-group social threats as well. However, the baboons underlying behaviours, foraging tasks, and feeding success predicted looking with the most precision. This suggests that whilst some behaviours appear to constrain opportunities for looking (e.g., grooming and digging), certain tasks (e.g., biting or handling food items) offer moments of compatible looking time that the baboons readily utilise. As a result, the study animals are likely to acquire useful and reliable information on their local threat environment regularly, and therefore may not be under consistent pressure to be pre-emptively vigilant for external threats. These results highlight that vigilance hypotheses can be explored using general definitions; however, research must consider numerous competing hypotheses within a single framework in order to understand the role that specific behaviours have in promoting and constraining looking.

Introduction

Vigilance, visually monitoring the surroundings for possible dangers and difficulties, is a widespread behaviour used by many animals to avoid costly encounters and interactions with threats (1). Early detection of threats can aid in avoiding life-threatening scenarios such as predation, antagonism with conspecifics, or conflict with humans. Owing to its critically important nature, the attention required to engage in vigilance typically limits how much time an animal can spend engaged in other fitness enhancing activities such as foraging (2). However, many group-living animals can circumnavigate these compatibility issues by diminishing their individual investment in vigilance activities as group-size increases; a phenomena known as the group-size effect on vigilance (3). The contrary prediction may be more applicable in species that experience within-group competition and conflict, however. In these scenarios, vigilance should increase as group-size increases (4) owing to the increased likelihood of encountering a threatening group-member. For example, dominance rank can also influence the vigilance patterns exhibited by group members in complex social systems (5).

These predictions are further complicated because groups of animals are rarely in a uniform spacing, with inter-individual distances (i.e., group cohesion) and spatial position (e.g., peripheral or central) often highly variable across group members at any given time; as a result, the inclusion of these factors can change how risk and vigilance predictions are structured (6). For example, an animal occupying a peripheral location (within a group) during a period of high inter-individual spacings likely has the highest possible risk of predation, as dilution (7, 8) and confusion (9) effects are minimal. This risk prediction changes if group density increases and inter-individual distancing narrows. Under these circumstances a predator may detect a number of group-members more easily i.e., encounter effect (10), but it is now faced with the complex task of predating on an individual whilst avoiding collective detection and defence from the group (11, 12).

Given these complex and conflicting predictions, several authors have attempted to tease apart several different forms of vigilance, for example social/non-social vigilance (13), or social/antipredator vigilance (14). Vigilance has also been broken down into subcomponents. For example, ‘induced vigilance’ has been used to describe vigilance that takes place during foraging time, whilst ‘routine vigilance’ is utilised during periods when an animal is not engaged in any other tasks (15). Alternatively, vigilance can be pre-emptive or reactionary depending on the whether the animal is aiming to detect danger before it presents itself or aiming its vigilance at a current threat (16). The clear drawback of this approach is a potentially endless list of subtypes of vigilance, in which the nuances defining each form can make cross-study comparisons very challenging (17). Although many of these distinctions have not been explicitly made by researchers, exploration into the reported findings and approaches highlights numerous subcomponents have now been explored (see table 1).

Table 1. Key drivers of risk in group living animals and the relevant type of vigilance used to monitor or avoid threats.

Driver of vigilance	**Risk theory**	**Type of vigilance**	**Example**
Presence of an extra-group threat	Risk higher in presence of threat	Reactionary vigilance (antipredator/extragroup)	(18)
Within-group conflict	Risk higher during conflict	Reactionary vigilance (within-group)	(19)[†]
Spatial cohesion (external threats)	Risk increases as group cohesion decreases	Preemptive vigilance (antipredator/extragroup)	(20)
Spatial cohesion (within-group threats)	Risk increases as group cohesion increases	Within-group (social) vigilance	(21)
Spatial position (external threats)	Risk increases at the periphery of a group	Preemptive vigilance (antipredator/extragroup)	(22)
Spatial position (conspecific monitoring hypothesis)	Risk higher in the centre/ at the front of a group	Within-group (social) vigilance	(23)
Visibility (visual obstruction hypothesis)	Risk increases as visibility decreases	Preemptive vigilance (all threats)	(24)
Visibility (protective cover hypothesis)	Risk increases as visibility increases	Preemptive vigilance (all threats)	(25)
Distance to cover (protective hypothesis)	Risk increases with distance to cover	Preemptive vigilance (antipredator)	(26)
Distance to cover (obstruction hypothesis)	Risk decreases with distance to cover	Preemptive vigilance (antipredator)	(27)
Landscape of fear (external threats)	Risk increases in high-risk areas	Preemptive vigilance (all external threats)	(28)
Range overlap (foreign conspecific groups)	Risk increases in areas of high overlap	Preemptive vigilance (foreign conspecifics)	(29)
Boundary areas (external threats)	Risk increases in areas close to boundary of home-range	Preemptive vigilance (all external threats)	(30)
Dominance	Risk higher for subordinates	Within-group (social) vigilance	(31)
Identity of neighbours	Risk increases with proximity of threatening neighbours	Within-group (social) vigilance	(32)
Time of day (predation risk)	Risk increases in lower light levels	Preemptive vigilance (antipredator)	(33)
Time of day (energetic demands)	Vigilance increases with increasing energy reserves	Preemptive vigilance (all threats)	(34)
Body size (all threats)	Risk higher for smaller individuals	Preemptive vigilance (all threats)	(35)
Reproductive state (Gestation/lactation period hinders escape ability)	Risk increases with gestation/lactation period	Preemptive vigilance (all threats)	(36, 37)
Reproductive state (Gestation/lactation period reduces energy levels)	Vigilance decreases with increasing energetic demands	Preemptive vigilance (all threats)	(38)
Maternal care (all threats)	Risk higher for females with infants	Preemptive vigilance (all threats)	(39)
Maternal care - infant age (all threats)	Risk decreases as infant age increases	Preemptive vigilance (all threats)	(40)
Maternal care - infant distance (all threats)	Risk increases with distance to infant	Preemptive vigilance (all threats)	(41)
Male consortship status (intra-sexual competition hypothesis)	Risk higher when mate guarding	Preemptive and reactionary vigilance (conspecific threats)	(42)
Observer distance (threat hypothesis)	Risk increases with observer proximity	Preemptive vigilance (all threats*)	(43)
Observer distance (human-shield hypothesis)	Risk decreases with observer proximity	Preemptive vigilance (all threats*)	(44)
Observer movement	Risk higher when movement occurs	Reactionary vigilance (observer)	(43)

[†] Conflict between conspecifics draws visual attention for individuals not engaged in conflict, which can compete with antipredator vigilance. *Potential for habituated animals to exploit within-group tolerance differential, therefore, tolerant phenotypes could perceive less risk when in proximity to observers.

Food intake rate and food availability may also have a governing role in the expression of these variables (table 1); animals foraging in areas with more food are expected to decrease investment in vigilance to maximise food intake rate (e.g., (45)). These predictions may change based on the sensory capacity an animal has during different postures, as some species are able to utilise their peripheral vision during foraging (46). Some species have the sensory capacity to detect localised threats during engaged behaviours such as foraging, despite not being overtly vigilant (47, 48). Conversely, it has also been shown that foraging tasks requiring increased attention and handling time can hinder threat detection substantially (47). Predictions about vigilance are therefore inextricably linked to a specific study animal's postures and sensory capacity, and the unique foraging tasks they encounter.

The most common approach to study this complex topic is to only investigate one or two types of vigilance, under a narrow set of scenarios, allowing a smaller and more manageable list of questions to be tackled independent of the remaining factors. This approach is popular, but it carries two principal drawbacks. Firstly, directly sampling different types of vigilance is challenging, especially in field conditions, as few animals flawlessly betray an internal state of vigilance or their precise focus of visual attention (1, 49). Secondly, testing hypotheses in isolation may be less helpful for disentangling these effects compared with methods that weight competing hypotheses. A preferable approach may be to develop a framework that explores numerous factors in unison, allowing researchers to gain a more intricate understanding of the relative weighting each factor has (e.g., (18)). So far, this approach has been underutilised, particularly in primate vigilance research (see supplementary material (17)).

With these issues in mind we previously presented the looking framework (17) where we postulated that under field conditions it is very challenging to precisely and consistently identity when an animal is performing specific vigilance behaviours (e.g., preemptive or social vigilance). Thus the proposed looking framework aims to avoid misidentifying specific vigilance behaviours by deliberately sampling all looking behaviours (17) across all behaviours and scenarios, and use the contextual information of each scenario to identify the most prominent trends analytically. Despite its generality, the looking definition should still allow the data to reveal which forms of vigilance are used in different contexts and lends itself to exploring multiple hypotheses concurrently (e.g., (18)).

In this study, we evaluated the scenarios plausibly linked with looking behaviours in a habituated group of gray-footed chacma baboons (*Papio ursinus griseipes*). We aimed to identify when and where elevated looking patterns consistently aligned with predicted risky scenarios whilst also incorporating several alternative, non-risk associated behavioural and compatibility hypotheses into the same framework (17). In order to identify and examine these competing hypotheses within a single analysis we employed an information-theoretic approach as described by Burnham, Anderson, & Huyvaert (2011) to create and compare a set of models representing biological hypotheses (see tables 1 and 2). We explored two dependent variables separately, frequency of looking bouts and total duration of looking bouts within focal observations. We adapted the IT-approach (50) for Bayesian models using a ‘stacking’ procedure. (51), whereby each model was weighted according to the predictive accuracy of the posterior distributions generated. We gave each response variable its own stack of 21 candidate models (see table 2), with each model exploring an independent hypothesis potentially applying to this study group. This framework enabled us to disentangle the various subcomponents of vigilance (e.g., social vigilance, preemptive vigilance for predators, observer vigilance etc) from non-risk driven looking patterns and weigh them according to their relative prediction accuracy.

We fitted an intercept only model (see table 2: *Model 1*) as this offered an important candidate model for comparison within each stack, if it yielded greater prediction accuracy than other models it would suggest the independent variables were poor predictors of looking. Some of the most common themes explored in primate vigilance research are differences in vigilance use across sexes (e.g., (30, 42), ages (e.g., (52–54)), female reproductive states (e.g., (40, 52, 55)), and infant conspicuousness/proximity to mothers (e.g., (4, 40, 41)); and differences in vigilance use between different behaviours or activities (e.g., (26, 56–58)). Thus, our second model explored these hypotheses independent to other potential factors by including a variable for age-sex class (including distinctions between adult females without dependent infants, with their dependent infant in proximity, and with their dependent infant out of sight), and a variable for time spent engaged/not engaged. These models are described as our minimal models as both variables were also included in all other candidate models to account for their role in governing looking patterns. Time spent engaged (i.e., grooming, digging, picking fruit) was used as a predictor for all frequency of looking models, and time spent not engaged (i.e., resting, receiving grooming, handling) was used for all models using the duration response variable. For most hypotheses if time spent ‘engaged’ is high then the expectation is that frequency of looking bouts become the more risk-sensitive response variable. Whereas duration of looking bouts is a more risk-sensitive response variable when time spent ‘not engaged’ is high.

As highlighted in table 1, spatial position and cohesion hypotheses can make competing predictions depending on whether threats are from internal or external group threats. To explore these hypotheses, we included candidate models exploring the interactive effect of number of neighbours within five meters and spatial position (i.e., central or peripheral) of the focal animal on both the frequency and duration of looking bouts (see table 2: *Model 3*). Thus, both models (one for each response variable) explore the external threat hypothesis, i.e., risk is highest when an animal is peripheral and the group is sparse, and the conspecific risk hypothesis, i.e., risk is highest when central and the group is cohesive (see table 1).

Primate vigilance research is made challenging by differing postural tendencies and handling abilities of each species, with evidence suggesting time spent using vigilance is tied to the ratio of search time and compatible handling time (59). Some food items such as roots can require handling to clean dirt away before consumption, whilst certain fruits and seeds require a different form of manual processing where the teeth are used to crack open a hard casing or to peel off the skin of a fruit; as the eyes are not necessarily needed for the processing task, the animal may be able to briefly scan their surroundings whilst biting. These tasks may offer compatible or cost-free looking time (15), and looking behaviours may not need to be risk sensitive in these scenarios and could potentially also hold a positive correlation with looking bouts, i.e., foraging success could ‘promote’ the frequency of looking bouts for certain food items. Each response variable therefore included a model (see table 2: *Model 4*) to specifically explore the association between looking patterns and the predominant food item consumed during the focal observation, and additionally, the relationship between foraging success (i.e., number of bites or items placed in the focal animal’s mouth) and both looking variables.

Each response variable also included a model (*Model 5*) designed to explore whether specific behaviours are associated with consistent patterns of looking behaviours, e.g., as handling time increases (regardless of the specific item) the duration or frequency of looking may increase. Primates can also be engaged in tasks such as auto-grooming and allogrooming which may lead to decreased investment in looking or vigilance as monitoring could be shared between partners or could have a calming effect on both individuals (58). As baboons utilise a range of postures (see (60)) we also included the focal animal’s predominant posture during the focal observation within the specific behaviours models, i.e., sitting, laying, or standing (quadrupedal or bipedal). Although models 4 and 5 do not explore specific risk drivers of looking, both are important alternative hypotheses for understanding the scenarios that promote or constrain looking generally. For example, animals may not need to be pre-emptively vigilant if they readily utilise cost-free or compatible moments of looking time during certain behaviours (17).

Despite several studies noting the important differences between induced and routine vigilance (15, 61) or preemptive and reactionary vigilance (52), many primate research studies overlook this key distinction (17). We included a set of candidate models (table 2: *Models 9 – 14*) that describe whether certain events are ongoing and the time since these events ended. These events included non-threatening within-group stimuli (e.g., copulations, female ‘lost’ calls), potentially threatening within-group stimuli (e.g., male wahoos and within-group aggressions), passive and active heterospecific encounters (e.g., bushbuck walking past the group or warthogs charging group members), group-wide alarm episodes (e.g., during leopard encounters), encounters with domestic dogs, and encounters with other groups of baboons. Non-threatening events can still draw visual attention and therefore potentially lead to increased looking, as such they are important to explore within a looking framework as overlooking them could lead to important information being missed.

The counterpart to reactionary vigilance, preemptive vigilance, has received more attention in primate research ((17); table 1). Although risk is typically perceived to be from predators, for group-living species experiencing contest competition for resources, within-group threats may pose a greater risk to fitness (62). Although social vigilance has received a lot of attention in primate vigilance research, numerous variables have been used as proxies for threats, including distance to nearest neighbours (63), number of neighbours (21, 57), rank of neighbours (31, 56), and relationship to neighbours ((64, 65). Model 15 (see table 2) explores the patterns of looking behaviours in response to changes in the number of social threats within five meters of the focal animal. We considered social threats to be any individual ranked higher than the focal animal who was not part of their social 'clique' (as identified from a grooming data).

Our next set of models (*Models 16 – 20*) explore the remaining preemptive vigilance scenarios. This included the spatial likelihood of encountering leopards (see (66, 67)), the likelihood of encountering other groups of baboons (e.g., (66, 68)), home-range familiarity (e.g., (30)), and habitat type. We explored the effect of home range familiarity on looking using a continuous and a categorical variable. Habitat type allowed exploration into how the baboons may perceive fear differently according to specific human infrastructures such as farms and researcher camps. For example, camp settings may offer baboons safety from leopards, whilst farms may reduce leopard risk at the cost of proximity with unfamiliar and potentially threatening humans. This additionally allowed exploration into whether they perceive risk differently across broadly classified vegetation types including grassland, bushland, woodland, and forests, as leopards are known to preferentially utilise densely vegetated areas at Lajuma (67).

Primate vigilance literature has typically focused on predators and conspecifics as the major drivers of vigilance in primate groups, with little work exploring the role of humans (although see (69)). An implicit assumption in research using direct observations of habituated animals is that the study subjects no longer fear observers and view them as neutral stimuli; however, our previous results challenged that these assumptions applied to our study group (48). We also found an individual-level tolerance trait had emerged, whereby the study animal's did not appear equally tolerant to observer approaches (48). These individual tolerance levels were consistent across two observers differing in familiarity and across a range of scenarios, including after a predation event from a leopard (70). When researchers were within 4.5 meters of focal subjects, we also found a positive association between tolerance and how often an individual occurred as a neighbour to focal animals, i.e., very intolerant animals avoided proximity to researchers (71). In our final model (table 2: *Model 21*), we explore whether interactions between tolerance level and observer distance, and tolerance and observer movement, during observations influence looking patterns.

Visibility was included as a predictor in several models (see table 2: *Models 6, 9, 10, and 12 – 20*) to account for the competing predictions of the protective cover hypothesis and the visual obstruction hypotheses (see table 1), and therefore was not used in minimal models, or models exploring non-threatening stimuli. As with visibility, the dominance rank of the focal individual was also included as a predictor in all models exploring risk hypotheses to account for possible rank effects on looking and vigilance behaviours (e.g., (72–74).

Methods

Study area

All data was collected on a wild habituated group of chacma baboons (*Papio ursinus griseipes*) at Lajuma Research Centre, western Soutpansberg Mountains, South Africa (central coordinates S29.44031°, E23.02217°) between May 2018 and July 2019. The study area was designated Afro-montane mist-belt community and contained a diverse range of natural habitats varying in plant species composition, canopy height, and foliage density (75, 76). Most of the study area was classified as private nature reserve, but agricultural practices and habitat modification took place in adjacent areas within the core area of study group's home range (77). Known predators of the baboons in the study area include leopards and rock python, whilst the study group have also been observed to act fearfully and alarm call at brown hyena, honey badger, and occasionally towards a number of raptor and corvid species.

Study group

The study group has been habituated for research purposes since 2005, for more detail on research history and typical observation schedules see Allan et al., (2020). At the onset of the study the group contained 80 individuals and despite a small number of adult and adolescent disappearances, the group had grown to 92 individuals by the end of the study, this increase was purely from births as no permanent immigrations took place. In total 65 individuals were used for the analysis. The individuals sampled in this study occupied all age-sex classes except for infants (see supplementary information S1 for age-sex class and mother-infant proximity descriptions). If a small juvenile was nutritionally independent at the beginning of the study it was included, however, if an individual was classified as a neonate or infant at the beginning of the study (nutritionally dependent, infant pelage etc) then it was not incorporated into the focal observation as it matured. Animals that were present at the beginning of the study but disappeared during the study period were removed from the main focal looking analysis (see below), however, their influence on focal animals (i.e., as a neighbour) was still explored for the periods they were still in the group.

Video sampling methodology

30-second continuous focal sampling was used to measure the looking behaviours of the study animals (see chapter 3 for full description and justification), a high-definition video camera was used to record all focal observations (Panasonic HC-W580 Camcorder). Continuous sampling was used to ensure the temporal organisation of looking behaviours was recorded (1, 17, 78).

Each observation day was split into four seasonally adjusted time-periods that each accounted for 25% of the current day length. A list of the focal individuals was ordered alphabetically in an Excel spreadsheet and each individual allocated a random number, subsequently this list was sorted by the random number to create a 'randomly' generated order. Focal individuals were then selected pseudo-randomly from this list by sampling the first individual encountered from the top 15 identities on the list (approximately 20% of original group-size). 3676 focal observations across the 65 study subjects (range: 54 – 59 per individual) were used in this analysis. More were completed in situ but required removal from the data due to individuals dying or emigrating. Some observations were excluded during the video-coding phase (see below) due to issues with video quality.

Focal observations were considered successful if at the end of a sample it was likely that there was at least 25 seconds of footage recorded with at least 50% of the animal's face in view. If during the observation it felt like greater than 50% of the focal animal's face was out of sight for more than 5 seconds, then the observation was aborted. In these scenarios AA would then adjust position and try to restart the focal observation, this was repeated a maximum of three times, after which AA would move to another individual from the list. The individual receiving the aborted focal would then be reintegrated at the end of the list. After extracting looking behaviours from video footage only one observation occurred with less than 25 seconds with at least 50% of the focal animal's face in sight (24.639 seconds), we retained this observation as 'time in sight' was controlled for analytically (see *statistical analysis*).

Extracting looking information from video-footage

Using the video playback software Media Player Classic (MPC-HC: Guliverkli project), videos were slowed down to extract precise looking bout lengths (video skip length could be reduced to 4 hundredths of a second when played back at quarter-speed). If the focal animal was deemed to be looking at the start of the focal observation, then looking was considered to start at the same time as the observation period. A looking bout began when the focal animal's eyes were open, and its line of vision extended beyond its hands and the substrate, animal, or object its hands were in contact with. The substrate usually refers to the ground but could also include rocks or branches the baboons were sitting or standing on or moving across. A looking bout ended when the focal animal diverted its line of vision towards an item in contact with their own hands, e.g., focal animal's own body, foraging substrate, the ground (or another substrate they are sitting or standing on), or another monkey; or the animal closed its eyes. When animals were in contact with or facing large objects within an arm's reach (e.g., tree trucks, rocks, buildings etc.,), these objects were considered an extension of the substrate, therefore, the animal had to divert its line of vision away from its hands and the object to be considered looking.

Contextual variables

During the video focal observations undertaken in the field, AA recorded a number of contextual factors that were used as predictors within a range of candidate models (see table 2). The factors assessed at the beginning and end of the focal observation included the number and identity of all neighbours within 5 meters of the focal animal, the estimated visibility (percentage) to 5 meters in all directions from the focal animal (see supplementary material S2 for detailed methods), and the distance between the focal animal and the observer. All three variables were averaged across the start and end assessments so that each focal observation had a single value for each variable.

A number of additional variables were recorded at the end of the focal observation. We recorded habitat type as one of: forest, woodland, bush, grassland, rock, and roads, for full descriptions see supplementary material S3 (text S2). Cliffs were incorporated into the other categories according to the underlying substrate or vegetation structure (e.g., rock, grassland). We also used this variable to define additional anthropogenic categories of camps and farms. Both areas are highly modified at the field site, both camps and farms likely deterred leopards; however, farms posed a unique risk with workers typically acting hostile towards the baboons (chasing, shouting, throwing stones etc). Forest, woodland, and bush habitats were all associated with higher NDVI (normalised difference vegetation index) values which predicts a higher probability of leopard occurrence in the study area (67), and therefore should represent higher risk areas for the baboons. We did not investigate focal animal height in this study as it was challenging to complete observations on animals high above the ground due to visibility, practicality, and safety concerns, thus focal samples are biased towards locations relatively near to the ground.

The focal animal's spatial position was assessed as whether the animal was within the centre or the periphery of the group for the majority of the focal observation. This was determined via assessment of visual and audible cues given by other group members. An individual was peripheral if on the edge of the group or had no more than 5 non-infant individuals between itself and the edge of the group. AA also noted reproductive information for the focal animal, including consortship information and female cycle status (e.g., sexual swelling present, not cycling, lactating/infant carrying, pregnant etc). For lactating/nursing females the age-sex class of their offspring was noted, and the distance to offspring was noted (unless it was out of sight of its mother).

We used the focal videos to record the duration of each behaviour exhibited by the baboons. Engaged behaviours were all behaviours requiring visual attention and use of the hands, including grooming another individual, auto grooming, digging, searching substrate (e.g., leaf litter, wafting grass, rock rolling, fanning dirt), and picking. Picking was the action of picking or pulling small fruit, seeds, grass blades etc., toward their mouths and would often lead to the entire item being consumed without further processing. However, if the item was bitten or manipulated further, then the picking bout would end and a handling or biting bout would start.

Not engaged behaviours included resting, chewing (including cheek pouch use), mating, self-scratch, receive grooming from another individual, movement (non-foraging or aggression), communication (e.g., facial gestures and greetings), drinking, biting, and handling. Biting was defined as when animals take several smaller bites of large fruits (e.g., lemon), seed pods, large roots, or succulent leaves, instead of placing whole item in their mouth (i.e., 'picking' small fig fruits), this biting action likely allows for compatible looking time. Handling involved the action of cleaning dirt off of roots or the use of their fingers to peel or pull open casings of some thick-skinned fruit or seed pods or pick off wings/legs of invertebrates. AA updated the food species and food item during the focal observations and assessed foraging success (total number of bites taken and items consumed during the observation) during video playback.

Aggression/play (chasing, fighting etc.) were also recorded and considered engaged behaviours but were not investigated within the specific behaviours model (see table 2: model 5) as they were under sampled. Communicative gestures, drinking and mating observations were also rare and therefore were not investigated within the specific behaviours model but were included in time spent not engaged calculations. Both total time spent engaged and time spent not engaged were included in the specific behavioural models to account for the time devoted to these behaviours.

Finally, it was noted whether certain events were ongoing during each focal observation, including within group events such as copulations and aggressions, and loud vocalisations, such as those made by females (e.g., lost calls) when the group was very dispersed and by males (i.e., wahoos) during a range of scenarios. Alarm calls were recorded as distinct to other vocalisations. Although they were often acoustically recognisable in this group, we only recorded them as alarms if there were additional behavioural responses (e.g., fleeing behaviours, screaming) or the threatening stimuli was identified (e.g., predator, worker throwing stones).

Encounters with other species were coded based on whether the event was considered passive or active. Passive encounters with other species included other animals (e.g., bushbuck, warthog) coming within 10 meters of a group-member with no detectable behaviour change or interaction between the two species, i.e., mingling. Active encounters occurred when some form of displacement or agonistic interaction occurred between the two species. For example, numerous encounters between warthogs and baboons contained supplants from warthogs towards baboons for food patches, whilst fighting was frequently observed with samangos. All encounters between the study group and leopards were grouped within the 'alarm' category due to threat level and only six encounters being identified. Encounters with domestic dogs were coded separately to other factors and did not have a passive/active distinction as dogs always chased or barked at the baboons. We also recorded encounters with other baboon groups but grouped passive (e.g., distant visual contact) and active (e.g., agonistic interactions) encounters as all encounters elevate the threat level. Throughout the day AA continuously updated the time each of these events appeared to end, allowing us to calculate the minutes since each event ended to explore the residual effect these factors have on looking patterns. Time since each event was coded accordingly: no event (on observation day thus far), event ongoing, 0-5 mins post event, 5-10 mins post event, 10-15 mins post event, and greater than 15 mins post event.

Calculating dominance rank and social risk

Aggressions, and displacement/supplant events were recorded ad libitum, then combined and manipulated into separate directed matrices for 2018 (n = 638 observations) and 2019 (n = 695). These matrices were then used to calculate dominance rank for each year using the *isi13* function from the *compete* package (79). Individual rank was then included as a covariate in several models (see table 2). Aggressions included fighting, biting, lunging, chasing, pinning down etc. An aggression was scored for the individual who was either the initial aggressor, or the most common aggressor during an interaction. In the rare case that both individuals seemed equally aggressive they were each scored against one another. Displacements were anytime an animal’s movement led to another individual moving away but, the actor did not take the place of the recipient. Supplants were when an actor approached a recipient (often to scrounge a food patch), with the recipient moving away and the actor taking a spot within 1 meter of the recipient’s location, this interaction could be active (e.g., grunting) or passive.

The dominance rank information was then applied to the identity of all neighbours within 5 meters for the focal observations used in this study, producing a count of higher ranked neighbours (with respect to the focal animal) calculated for each focal observation. For example, if an individual had four neighbours within 5 meters but only two were higher-ranking, the focal observation was scored as having two higher-ranking neighbours.

In many cases higher-ranking neighbours could still be affiliated with the focal animal, in which case these higher-ranking neighbours are unlikely to be considered threatening. It was therefore necessary to tune the number of social threats variable to each individual and focal observation such that it was not biased by affiliates. As such for each individual focal observation, the specific focal animal had their personal threat environment calculated, i.e., count of threatening individuals, which was the number of higher-ranked neighbours minus the number of higher ranked clique members. Clique membership was calculated using community detection in igraph with the spinglass algorithm (80). The spinglass algorithm allows cliques to be formed even when certain members are not consistently observed interacting but are grouped as they share close associates. For example, A – B, C -D, E - A, F – C, may all be very consistent dyads, but observations of B – C, D – A, F – A, etc., are rare. The spinglass algorithm can detect the clusters, i.e., connection chains, placing these individuals in the same clique. This meant that instead having numerous mother-offspring only cliques, we had cliques involving several related adult females and their associated offspring, and the adult males that consistently associated with them.

We used dyadic grooming interactions as the association measure for community detection, such that individuals are unlikely to be considered a threat if they share consistent grooming interactions. We used ad libitum sampling to record grooming interactions, for all grooming events the identity and direction of the interaction was recorded and later used to create directed matrices for 2018 and 2019 separately. This grooming data was collected outside of focal observations allowing observer effects on inter-individual association patterns to be minimised as AA could stand further away when collecting the grooming information than for focal sampling (see (71)). Clique membership was updated for each year to reflect changes in affiliative tendencies due to reproductive cycles, consortships, births, and deaths. We decided to keep grooming information recorded during consortships in these analyses as they reflected important aspects of the baboons ongoing behaviour and likely had a key role in social threat perception, e.g., adult females likely do not consider a regular consort partner a threat. On two occasions adult males were grouped in the same clique. Their focal observations were updated such that they should still consider the other male to be a threatening individual.

Spatial variables

Between February 2015 and July 2019, AA and research assistants collected ranging data for the study group and encounter data for all interactions with other groups of baboons or lone males (i.e., foreign individuals). Ranging data consisted of marking GPS points every 20 minutes throughout full day follows, e.g., 06:00, 06:20. 06:40 etc, producing n=11936 GPS points. Encounters with other groups of baboons were marked using a GPS when the events occurred (n=240). Some of these events could be very brief, e.g., sighting a lone male on a cliff, or remaining in proximity to another group for several hours. During the longer episodes, additional GPS points were only updated if the groups became visually separated by some obstruction, e.g., mist, woodland, cliff, and then encountered each other again at least 5 minutes later. Additional GPS points were also recorded if the status of the encounter changed, e.g., a passive encounter became active.

All ranging GPS points were entered into local convex hulls analysis (T-LoCoH) (81) to calculate home range utilisation distribution (UD) across all years (i.e., one consolidated home range). T-LoCoH generalises the local convex hull procedure (i.e., LoCoH (82)) to incorporate time and space into local hull construction. We used the fixed-*k* method (set to 24) to identify the nearest neighbours of each point and set the time scaled-distance metric set to 0.01, to ensure correct construction of isopleths (82). These values were selected with the aid of the graphical procedures available in the *tlocoh* package which allowed assessment of how different values minimised spurious holes and captured density gradients within the home range (81).

For the home-range familiarity continuous variable, the utilisation distribution was defined as the 99% isopleth and intensity of use calculated at 1% intervals. We applied a linear stretch to rescale the utilisation distribution predicted values between 0 and 1 according to (83), whereby each pixel value had the minimum UD value subtracted and the result divided by the maximum UD value minus the minimum UD value. For this analysis the scaled UD value was inverted (multiplied by minus 1) so that the hypothesized positive relationship between risk and vigilance could be visualised appropriately. For the categorical variable (for home-range familiarity), we defined the isopleths at $33.\dot{3}$% intervals to explore whether distinct differences between core, frequently used, and boundary areas influenced looking patterns. The number of GPS points for looking focal observations falling within these bounds was relatively similar: core areas – 1302 focal observations, frequently used areas – 1352, boundary areas – 1022.

We used the same methods (as with the utilisation distribution at 1% intervals) to calculate and scale the distribution of within-group encounters during the same period. In this case the time-scaled distance metric was set to 0 to reflect GPS points being collected opportunistically. The subsequent distribution was then scaled (as above) and divided by the scaled UD to produce a layer providing a proxy for spatial probability of an intergroup encounter, offset by home range utilisation, this variable was scaled a further time to ensure all values were between 0 and 1.

To explore whether the study group altered their looking patterns pre-emptively in response to varying spatial risk of encountering leopards, we used the scale integration (see (83)) of the 2nd and 3rd order resource selection function calculated by (67) for leopards utilising the same study area as the study group of baboons. Previously we have used solely the 3rd order RSF to explore preemptive vigilance hypotheses in this group (see (66)). Yet, the scale integration of multiple functions should be an improvement upon this as it incorporates additional environmental information (such as ruggedness and the slope of the landscape) which could have an important role in determining the probability of encountering a leopard. Initially a linear stretch was applied to each RSF to rescale their predicted values between 0 and 1, after which the scale probabilities of each pixel were multiplied (i.e., *P* (2nd order RSF) x *P* (3rd order RSF)), and finally scaled again using the linear stretch equation, resulting in scale integrated RSF layer (83), which represents the spatial probability of a baboon encountering a leopard. All spatial layers are shown in supplementary information S4 (figures S2 – S6).

Quantifying visual tolerance

To explore the role of the observer and the observer's behaviour (distance and movement) during focal observations we also included a variable quantifying each individual's tolerance of the observer. This variable was known as visual tolerance and was calculated by extracting the individual-level effects (i.e., conditional modes) from a model exploring the visual orientation distance (VOD) responses of the study animals to approaches made by observers. VOD was previously found to be distinct amongst individuals and repeatable within each individual (48). We updated the investigation from our previous study to include age-sex class, dominance rank, and additional trial number information to ensure a range of confounding factors were incorporated into the final individual visual tolerance estimates (see supplementary material S5 for complete methodology). The updated model allowed us to extract conditional modes for each individual, these values represented their relative sensitivity to observer approaches and therefore should be an ecologically valid variable to include in analyses exploring looking/vigilance behaviours using direct sampling. For example, sensitive individuals may glance or increase monitoring effort if the observer is too close or moves during the observation. As such we explore the effect of observer distance and movement interacted with individual tolerance levels.

Statistical analysis

We examined the drivers of two dependent variables, duration of time spent looking and frequency of looking bouts within 30-second focal observations. Each variable was investigated in a separate array of models, all fitted using the brm function from the brms package (84). In all models the observation length was included as an additional offset variable, as the focal animal's face could go out of sight temporarily, which therefore required the sampling effort (i.e., exposure) to be modelled. Duration models utilised a Gaussian family with identity link, therefore the offset variable (duration of the observation that 50% of the animal's face was visible) was not transformed. Frequency models utilised a Poisson family with a log link, and so, the natural log of the offset variable was used.

As 30-second observations are likely to curtail longer duration bouts we created a variable to describe when observations were right censored. Observations were considered right censored when the duration of looking was equal to the duration of time at least 50% of the animal's face was in view. As such, right-censoring could occur when the animal's face wasn't in view for the entire 30 seconds, as the focal animal could still be looking for the entire duration at least 50% of its face was visible. This approach allows the model to predict accurately beyond the 30-second cut-off imposed by the sampling design. This was applied to the duration models only as the censoring issue applies only to long duration looking bouts. As it is impossible for duration to be less than 0 we defined a lower bound of 0 (i.e., truncated) to the posterior distribution to ensure data was modelled correctly. For all duration models, we allowed all parameters to be initialised at zero allowing the no U-turn sampler to efficiently produce a finite log posterior (84).

For all models we used the default Student-t priors (df = 3, mean = 0, scaling factor = 10) in brms for all model components, in the case of the standard deviations of group-level (i.e., random) effects these parameters are constrained to be positive and therefore a half Student-t prior is implemented. We assessed model fits via graphical posterior predictive checking by comparing our observed data to data simulated from the posterior predictive distribution of our models using the pp_check function (brms and bayesplot packages). In each case the simulated data from our models generated data that captured the vast majority of values in our observed response distribution and did not fail to account for large proportions of zeroes or censored values in our observed datasets. (85, 86).

Following the information-theoretic approach of Burnham et al., (2011) we developed a series of models designed to test the main theoretical drivers of looking (see table 2). No single risk model included more than one type of risk variable, allowing insights into whether certain patterns of behaviour (e.g., time spent engaged/not engaged, spatial position) can independently produce different influences on looking behaviour depending on risk type. Reactionary variables (e.g., time since aggression) did not contain any interactions (e.g., with spatial position) as the ongoing event should be a clear driver to exhibit changes in looking duration or frequency regardless of the animal's current behaviour or scenario. Preemptive risk factors (e.g., spatial risk of encountering another group) should be much more sensitive to behavioural and individual factors and therefore several 2-way interactions required consideration. For example, the interactions between leopard RSF and spatial position (central/peripheral), spatial cohesion (average number of neighbours within 5 meters), and current behaviour (e.g., time spent not engaged) are the key hypothetical drivers of risk sensitivity in preemptive scenarios, as opposed to simply whether the animal is in a riskier location. Theoretically most hypotheses could warrant 3-way interactions (or more) as well as random slopes over individual identity, but we did not pursue these options as the models would have become very complex and likely overparametrized/unreliable.

We estimated the pointwise out-of-sample prediction accuracy from each model using leave-one-out cross-validation (LOO) from the 'loo' package (87). 'loo' uses a Pareto smoothed importance sampling (PSIS) procedure for regularising importance weights when computing LOO (51). PSIS approximation reliability was confirmed by inspecting the estimated shape parameter $\hat{k}$ diagnostic values in the generalized Pareto distribution (51, 88). The LOO process uses n-1 sample points (focal observations) to tune a specific algorithm to predict the left-out point, allowing the n-1 samples to act as a training set for optimising the free parameters of the model and assess how well the tuned algorithm performs at predicting the left-out sample point. This process is repeated for the remaining samples and produces a test performance for all samples within each model, the resultant estimates therefore provide ordinal information about relative model prediction performance.

Bayesian stacking was undertaken using the 'loo_model_weights' function from the "loo" package. We developed a number of 'stacks' to explore the relative weighting of each hypothetical driver of looking. When comparing two (or more) models using stacking with PSIS-LOO values, stacking utilises the data produced from the PSIS-LOO procedures of each candidate model, and compares the performance and accuracy of each model at predicting each left out sampling point. To achieve a stacking weight of 1, a model needs to predict every left-out data point with greater accuracy than the remaining models in the stack. Thus, models with greater weight offer greater predictive performance over other models exhibiting lower weight (88). Frequency and duration models were kept in independent stacks (see table 2). The initial stacks for each response variable contained all theoretical models in their respective stacks. A subsequent stack was also computed for each response variable including only models that shared weight in the initial stacks.

Stacking works to optimise model weights jointly and therefore performs strongly if many models are similar. Similar models can share weights allowing more unique models to produce undiluted weights. As such, the model weights are not spread evenly across numerous candidate models sharing similar structure, instead the weights of these similar models will likely be combined towards the one exhibiting the greatest prediction accuracy. If a specific model (e.g., the habitat type interaction model) consistently predicted each left-out data point with the greatest accuracy then it would likely it would have a weight close to one, which would indicate this model provided accurate predictions for looking across a broad range of contexts. If a similar low weight was shared across a number of models it would suggest that the many hypothetical models share similar prediction accuracy, i.e., that the specific hypothetical drivers predict some sample points with accuracy but perform poorly at predicting looking behaviours across a broad range of scenarios. If the intercept only models and/or minimal models continue to share substantial weight in these stacks, then it would indicate the majority of candidate models are poor predictors of looking patterns.

Results

Stacking weights

The initial stacking weights for frequency models suggested that foraging success/items, specific behaviours, preemptive risk factors associated with habitat type and home-range familiarity (core, frequently used, and boundary areas), and the number of within-group threats held the greatest prediction accuracy, although a number of other models also shared lower weight (see table 2). When the models with at least 0.001 weight were re-stacked, the models exploring specific behaviours and foraging success/items shared 0.833 of the model weights. This suggests that the specific behaviours model was the best predictor of the frequency of looking bouts, however, the foraging success/items model still predicted a large number of points with greater accuracy. The models exploring within-group threats, habitat type, and home-range familiarity cannot be overlooked entirely given their initial weights. Yet, they clearly yield less predictive precision than models 4 and 5. The remaining factors are very unlikely to be consistent drivers of looking frequency as they did not consistently yield greater weight than the intercept model; and as such, there is little evidence to support the hypothesized risk drivers of looking in these scenarios.

The initial stacking weights for duration models suggested that specific behaviours, foraging success/items, time since wahoos, time since encounters with other baboon groups, and within-group threats held the greatest prediction accuracy for the total duration of looking, although a number of other models also shared lower weight. When the models with at least 0.001 weight were re-stacked, the models exploring specific behaviours, foraging success/items, time since male vocalisations, and time since encounters with other baboon groups/foreign individuals shared 0.892 of the model weights. These models were therefore considered to be the most accurate and consistent predictors of the duration of looking in the study group, although within-group threats may also be important considering its initial weighting. Interestingly, for both response variables the intercept only model shared weight in all stacks, indicating that a small number of sample points were predicted more accurately with the intercept only model.

There were several cases where models exhibited less weight after the stacks were simplified. This is as a result of the stacking procedure, whereby similarly performing models have their weight combined to the model exhibiting greater predictive accuracy (51). For example, for the frequency response variable the stacking procedure is likely combining the weights for within-group threats models (model 15) with other similar models using some of the same predictors (e.g., models 7, 9, 12, and 13). This indicates that the within-group threats model produces a predictive distribution with greater accuracy than these similar models but still has far lower prediction accuracy than specific behaviours and foraging success/items models. Thus, upon removal of numerous models with zero weight, the remaining weights are combined towards the foraging success/items and specific behaviours models, again reiterating their greater predictive performance with regards to the frequency of looking bouts.

Table 2. Stacking weights for models exploring the hypothesized vigilance drivers of looking for frequency and total duration of looking bouts. Weights closer to zero indicate lower predictive accuracy of a model. A weight equal to 1 would indicate that a model predicts every data point with more accuracy that the other models within the stack. Weights in bold highlight values above 0.1. Behaviour refers to the total time devoted to either engaged or not engaged behaviours. WE = within-species encounter, either time since an encounter with another group/foreign individual, or spatial risk of encountering another group. WGT = count of within-group threats within 5m of the focal animal. UD = the utilisation distribution (i.e., home range) value at the location of the focal observation. CFB = when the focal observation occurred in core, frequently used, or boundary areas of the study group's home range.

	Model	Frequency of looking bouts		Total duration of looking bouts	
		Weights	Shared weights	Weights	Shared weights
1	~1	0.065	0.041	0.002	0.001
2	Age-sex class + Behaviour (Minimal)	0		0	
Group geometry and cohesion					
3	Number of neighbours * Spatial position + Age-sex class + Behaviour	0		0	
Compatibility factors (specific behaviours and foraging success)					
4	Amount eaten + Food item + Behaviour + Age-sex class	**0.129**	**0.322**	**0.138**	**0.204**
5	Biting + Digging + Handling + Pick + Searching substrate + Give groom + Auto groom + Receive groom + Chewing + Rest + Self scratch + Movement + Posture + Behaviour + Age-sex class	**0.203**	**0.511**	**0.106**	**0.264**
Reactionary risks					
6	Time since Aggression + Age-sex class + Behaviour + Vis + Rank	0.026	0.059	0.042	0
7	Time since Mating + Age-sex class + Behaviour	0		0	
8	Time since adult female calls + Age-sex class + Behaviour	0.003	0.001	0	
9	Time since adult or adolescent male calls + Age-sex class + Behaviour + Vis + Rank	0		**0.139**	**0.295**
10	Time since active heterospecific encounter + Age-sex class + Behaviour + Vis + Rank	0.078	0.008	0.009	0
11	Time since passive heterospecific encounter + Age-sex class + Behaviour	0.006	0	0.056	0.004
12	Time since dog encounter + Age-sex class + Behaviour + Vis + Spatial position + Number of neighbours	0		0	
13	Time since alarm + Age-sex class + Behaviour + Vis + Spatial position + Number of neighbours	0		0	
14	Time since WE + Age-sex class + Behaviour + Vis + Spatial position + Rank + Number of neighbours	0.057	0	**0.152**	**0.129**
Within-group risks					
15	WGT + Age-sex class + Behaviour + Vis + Rank + Number of neighbours	**0.106**	0	**0.174**	0
Preemptive risks (spatial position/cohesion and landscape of fear for external group threats)					
16	Leopard RSF *(Number of neighbours + Spatial position + Behaviour) + Visibility + Rank + Age-sex class	0		0	
17	Habitat type *(Number of neighbours + Spatial position + Behaviour) + Visibility + Rank + Age-sex class	**0.112**	0	0.048	0.024
18	Inverted UD *(Number of neighbours + Spatial position + Behaviour) + Visibility + Rank + Age-sex class	0		0.026	0
19	CFB *(Number of neighbours + Spatial position + Behaviour) + Visibility + Rank + Age-sex class	**0.172**	0.057	0.086	0.079
20	Spatial WE *(Number of neighbours + Spatial position + Behaviour) + Visibility + Rank + Age-sex class	0		0.02	0
Observer risks					
21	Tolerance * (Observer distance + Observer movement + Behaviour) + Age-sex class	0.042	0	0	

Specific behaviours (model 4)

Time spent biting (e.g., fruits, seed pods, corms etc) was positively associated with frequency and negatively associated with duration of looking bouts (see table 3). Digging, searching substrate (wafting leaf litter or grass to search for various food items), chewing, and picking (fruits, seeds, grass blades etc) time did not appear to influence the frequency of bouts substantially but shared a strong negative relationship (except chewing which was positive) with the duration of looking. Handling time also had a positive association with frequency but a negative association with duration. Most grooming behaviours were negatively associated with looking behaviours, although there wasn't a clear trend between time spent receiving grooming and duration of looking. Time spent self-scratching was also associated with increased looking time, but there wasn't a significant relationship with frequency of looking. Time spent resting shared a negative relationship with frequency but a positive relationship with duration; whilst there wasn't a strong relationship between chewing and frequency but there was a strong positive relationship between chewing and duration. There were no clear associations between movement and either looking variable. The frequency of looking did not appear to be substantially different between sitting and standing (bipedal or quadrupedal) postures, however, the duration of looking was substantially lower when animals were laying down. These results highlight the constraints certain behaviours (e.g., grooming, digging, picking) have on looking patterns, but also highlight the compatibility that biting, and handling food items has with frequent but brief looking bouts.

Foraging success and foraging items (model 5)

There was a positive association between foraging success (number of bites taken or number of items consumed) and the frequency of looking, and a negative relationship between foraging success and duration of looking (see figure 1). See supplementary information tables S8 and S9 for full model summaries. The main food item consumed, foraged, or manipulated also had a clear role in both the frequency and total duration of looking behaviours (see figure 2). Frequency of looking was clearly at its lowest when no items were consumed, foraged, or manipulated/handled during the focal observation. Items typically processed using the teeth, i.e., A.si (*Acacia sieberiana* subsp. *woodii*) and D.ci (*Dichrostachys cinerea* subsp. *africana*) seeds, large fruits, corms, and succulent leaves, were associated with a greater frequency of looking bouts, consistent with biting behaviours allowing for brief moments of compatible looking time. A.si and D.ci seeds, Z.mu (*Ziziphus mucronate* subsp. *mucronata*) fruits and seeds, roots, and succulent leaves were all associated with lower durations of looking relative to when no foraging or feeding behaviours took place. Whilst duration of looking was highest when leaves, grass blades, and grass seeds were the predominant food item. Collectively these results suggest specific foraging tasks and their relative complexity, success, and compatibility with looking are key factors governing looking behaviours, in particular, the positive association between frequency of looking and foraging success reiterates that some foraging tasks may promote the use of brief looking bouts.

Table 3. Model summary results for specific behaviours predicting the frequency and total duration of looking behaviours. Upper and lower 95% credible intervals are shown within parentheses. Bold text highlight parameter estimates where the Cis did not overlap or include zero. All R-hat (Gelman-Rubin convergence diagnostic) were less than 1.01 suggesting accurate estimates of the posterior distribution. In all cases the bulk estimated sample size (bulk_ESS) was greater than 100 times the number of chains (i.e., bulk_ESS > 400) indicating the mean was efficiently sampled in all cases.

	Frequency					Duration				
	Estimate and CIs	Est.Error	Rhat	Bulk_ESS	Tail_ESS	Estimate and CIs	Est.Error	Rhat	Bulk_ESS	Tail_ESS
Intercept	**-2.27 (-2.68, -1.84)**	0.21	1.00	966	2006	**-23.52 (-30.41, -16.86)**	3.42	1.00	683	1345
Biting	**0.03 (0.02, 0.04)**	0.01	1.01	723	1373	**-0.28 (-0.48, -0.07)**	0.11	1.01	620	1390
Digging	-0.01 (-0.03, 0)	0.01	1.01	733	1380	**-1.2 (-1.44, -0.97)**	0.12	1.00	714	1502
Searching substrate	-0.01 (-0.02, 0)	0.01	1.01	717	1384	**-1.27 (-1.51, -1.04)**	0.12	1.01	704	1356

Chewing	-0.01 (-0.02, 0)	0.01	1.00	700	1389	**0.43 (0.23, 0.63)**	0.1	1.01	604	1295
Grooming give	**-0.04 (-0.05, -0.03)**	0.01	1.00	739	1492	**-1.66 (-1.92, -1.42)**	0.13	1.01	750	1617
Auto grooming	-0.02 (-0.03, 0)	0.01	1.00	798	1388	**-0.83 (-1.06, -0.6)**	0.12	1.01	703	1412
Handling food item	**0.02 (0.01, 0.03)**	0.01	1.00	744	1311	**-0.59 (-0.82, -0.35)**	0.12	1.00	740	1622
Picking	0 (-0.01, 0.01)	0.01	1.01	686	1346	**-0.95 (-1.15, -0.74)**	0.11	1.01	614	1380
Receive grooming	**-0.03 (-0.04, -0.01)**	0.01	1.00	763	1644	0.12 (-0.08, 0.32)	0.1	1.01	589	1313
Resting	**-0.02 (-0.03, -0.01)**	0.01	1.00	723	1455	**0.3 (0.1, 0.51)**	0.1	1.01	594	1392
Scratching	0.01 (0, 0.03)	0.01	1.00	999	2143	**0.34 (0.07, 0.61)**	0.13	1.00	849	1502
Movement	0.01 (0, 0.02)	0.01	1.00	761	1452	0.09 (-0.11, 0.31)	0.11	1.01	660	1390
Posture (Sitting)	0.08 (-0.12, 0.29)	0.11	1.00	4981	3293	**11.08 (8.55, 13.68)**	1.3	1.00	3032	2775
Posture (Standing)	0.17 (-0.04, 0.38)	0.11	1.00	5030	2911	**12.22 (9.55, 14.9)**	1.36	1.00	3023	2656
Adolescent males	-0.18 (-0.37, 0)	0.09	1.00	2795	3024	0.71 (-2.14, 3.62)	1.49	1.00	2042	2563
Adult females	-0.07 (-0.18, 0.03)	0.05	1.00	1518	2238	-0.68 (-2.56, 1.21)	0.94	1.00	1208	1960
Adult females (Infant contact)	-0.02 (-0.14, 0.11)	0.06	1.00	1851	2666	-0.81 (-2.99, 1.35)	1.12	1.00	1332	2204
Adult females (Infant OS)	-0.01 (-0.25, 0.21)	0.12	1.00	4098	2891	-0.26 (-4.87, 4.38)	2.36	1.00	3575	2639
Adult males	**-0.21 (-0.35, -0.07)**	0.07	1.00	1846	2583	0.3 (-1.89, 2.46)	1.1	1.00	1464	1992
Juvenile-1 females	0 (-0.14, 0.14)	0.07	1.00	2110	2542	-0.37 (-2.93, 2.09)	1.25	1.00	1720	2144
Juvenile-1 males	-0.12 (-0.27, 0.02)	0.07	1.00	2057	2667	-0.55 (-2.92, 1.9)	1.23	1.00	1376	1957
Juvenile-2 females	-0.02 (-0.14, 0.1)	0.06	1.00	2542	2894	0.41 (-1.8, 2.64)	1.14	1.00	1937	2618
Juvenile-2 males	-0.08 (-0.2, 0.05)	0.07	1.00	1782	2583	0.75 (-1.33, 2.88)	1.07	1.00	1173	1722
Juvenile-3 males	**-0.18 (-0.33, -0.03)**	0.08	1.00	1923	2824	0.05 (-2.43, 2.55)	1.25	1.00	1634	2636
Date						Date				
sd(Intercept)	0.08 (0.04, 0.11)	0.02	1.01	1369	1760	0.7 (0.04, 1.34)	0.34	1.00	739	703
ID						ID				
sd(Intercept)	0.11 (0.08, 0.15)	0.02	1.00	1758	2939	1.45 (0.9, 2.05)	0.3	1.00	1550	2233
Family						Family				
sigma						7.95 (7.64, 8.27)	0.16	1.00	3147	2615

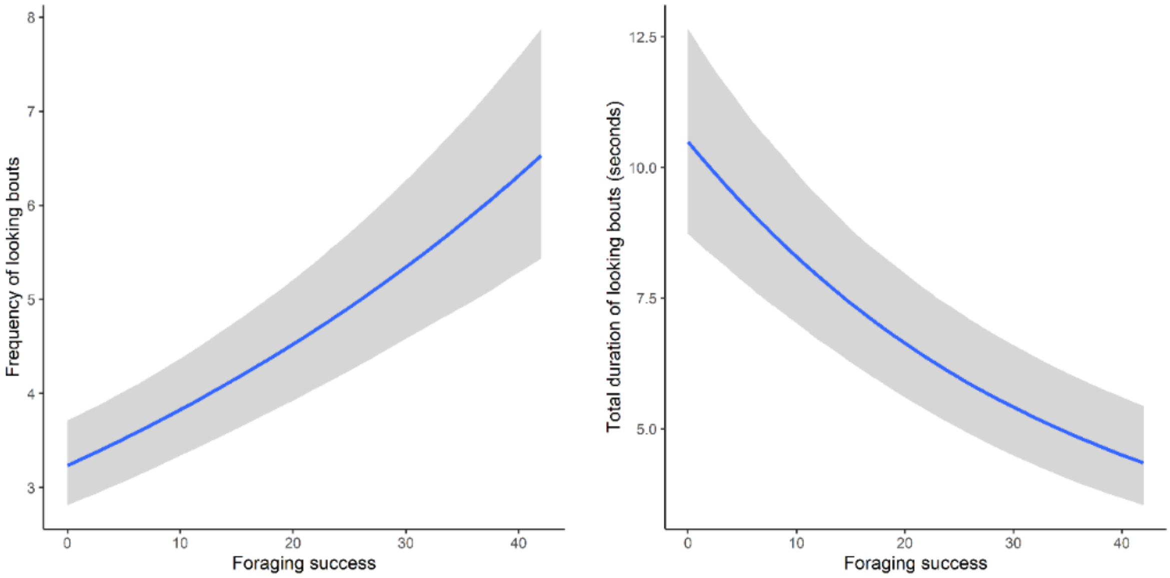

Figure 1. Conditional effects plots displaying the relationship between foraging success (i.e., number of bites/items consumed within a 30-second focal observation) and the frequency and total duration of looking bouts. Shaded areas display the relevant credible intervals (2.5% and 97.5% quantiles).

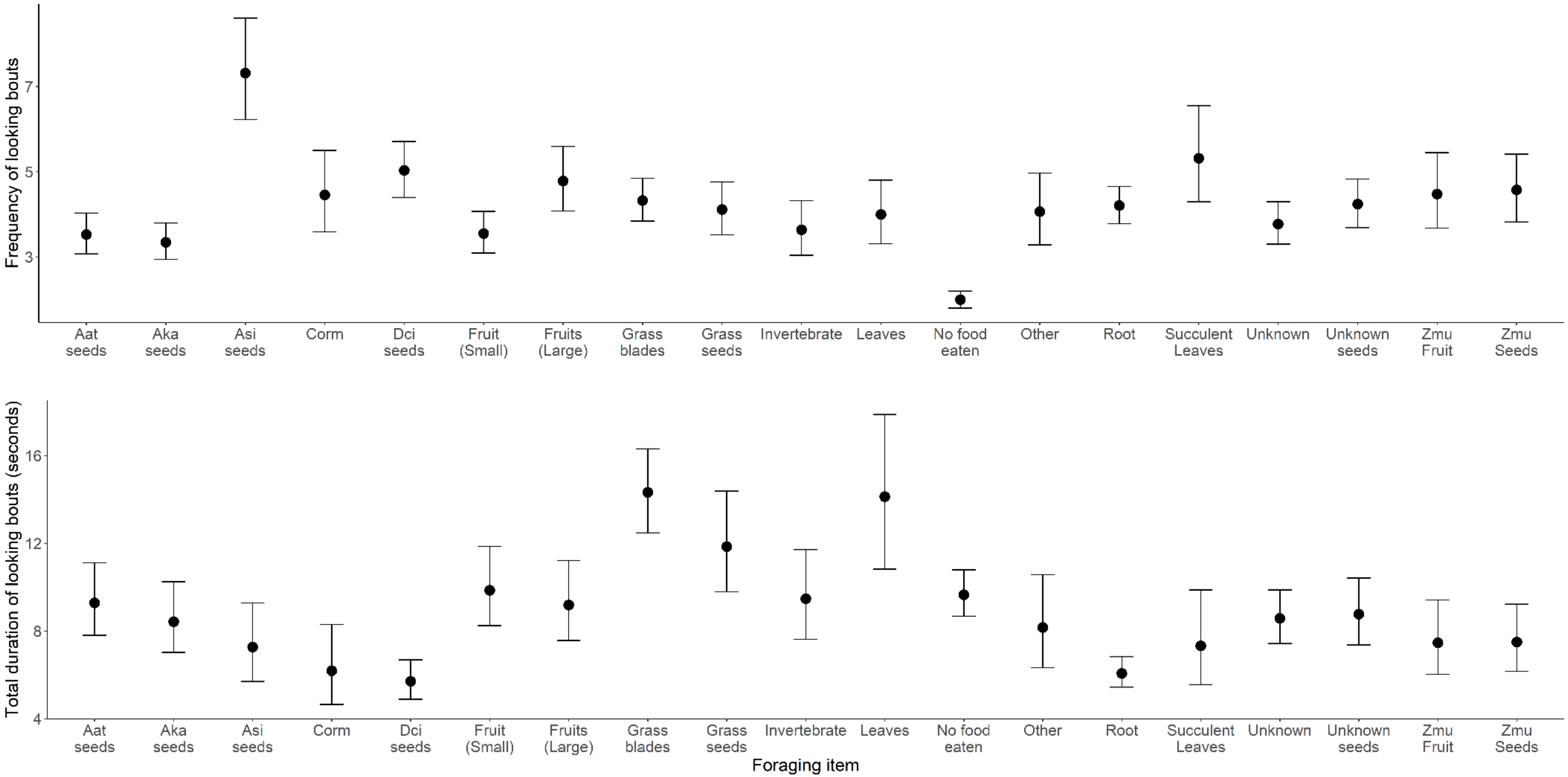

Figure 2. Conditional effects plots displaying the relationship between the predominant foraging item searched for, manipulated/handled, or consumed (during a 30-second focal observation) and the frequency and total duration of looking bouts. Dots display parameter estimates and bars display the relevant credible intervals (2.5% and 97.5% quantiles). Aat refers to *Acacia/Senegalia ataxacantha,* Aka: Acacia/*Vachellia karoo*. Small fruits could be placed in a baboon's mouth whole whereas large fruits required several bites or manipulation. No food eaten refers to no food being consumed or foraged for during the focal observation. Other were rarer items grouped together, including fungi, bamboo shoots, and animal matter. Succulent leaves included numerous *Aloe spp* and *Opunita ficus-indica.* Unknown was when the focal animal picked or consumed something the observer could not identify. Unknown seeds were seeds taken from the ground/leaf litter where it was clear seeds were being foraged but the precise identity of the species not known.

Reactionary risk models (models 6 – 14)

When modelled using the frequency response variable no reactionary models held considerable weight, with only the time since active heterospecific encounters model yielding greater prediction accuracy than the intercept only model. When modelled using the duration response variable, time since male vocalisations (i.e., wahoos) and time since encountering another group or foreign individual held greater than 0.1 weight regardless of the models included in the stack, suggesting both scenarios resulted in consistent behavioural responses. In both cases, the total duration of looking bouts was greatest whilst events were ongoing (see figure 3). When these events were not ongoing the total duration of looking bouts appears consistent across the remaining time categories, including when no event had occurred during an observation day. This indicates the study animals had a strong reactionary vigilance response to these stimuli but reverted to typical patterns of behaviour very quickly. See supplementary material for model summary results for all reactionary models (tables S10 and S11).

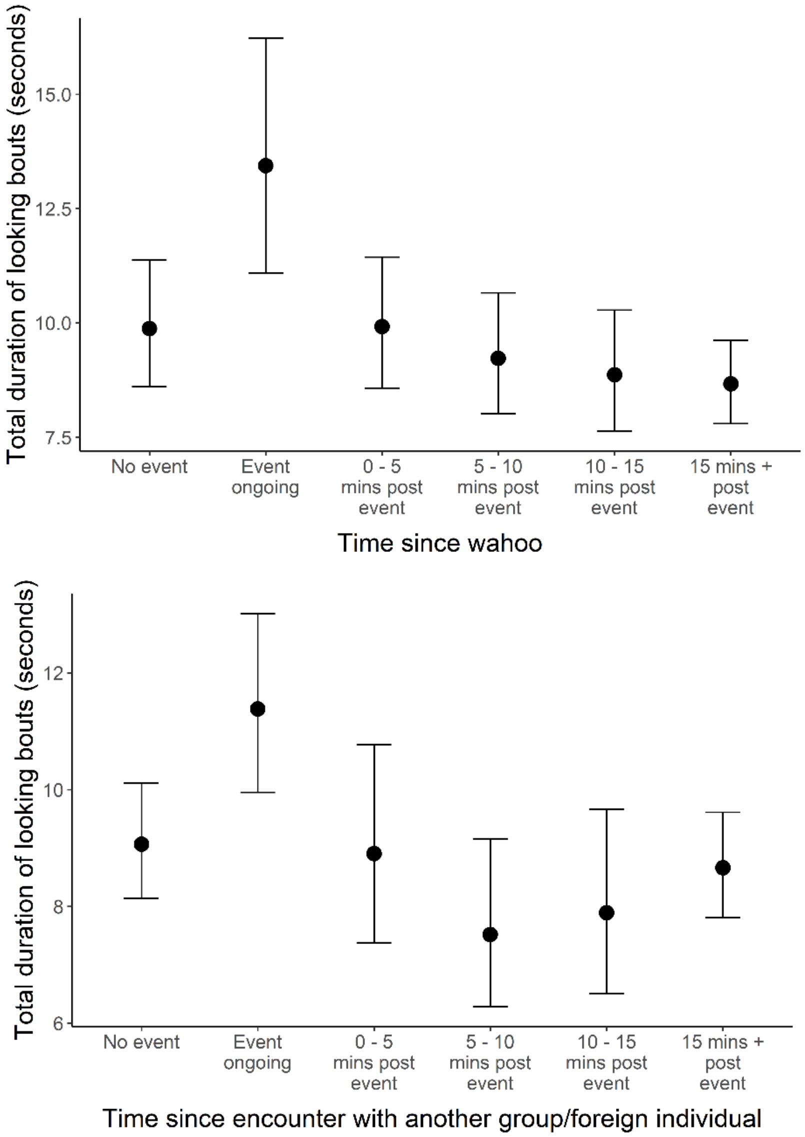

Figure 3. Conditional effects plots displaying the relationship between the time since an event and the total duration of looking bouts. Dots display parameter estimates and bars display the relevant credible intervals (2.5% and 97.5% quantiles).

Within-group risk (model 15)

For both frequency and duration models there was a positive relationship between the number of social threats within 5 meters and looking (see figure 4). See supplementary material (tables S12 and S13) for full model summary results. Interestingly, the relationship between looking patterns and the number of social threats is opposite to that found between looking behaviours and number of neighbours in the same models (see S12 and S13). As the social threats variable was tuned to each individual, these results indicate that the focal animals were attentive to the identity of their neighbours and often increased their looking behaviours if their individual-specific risk increased, regardless of the potential reduction in risk experienced when number of neighbours increased.

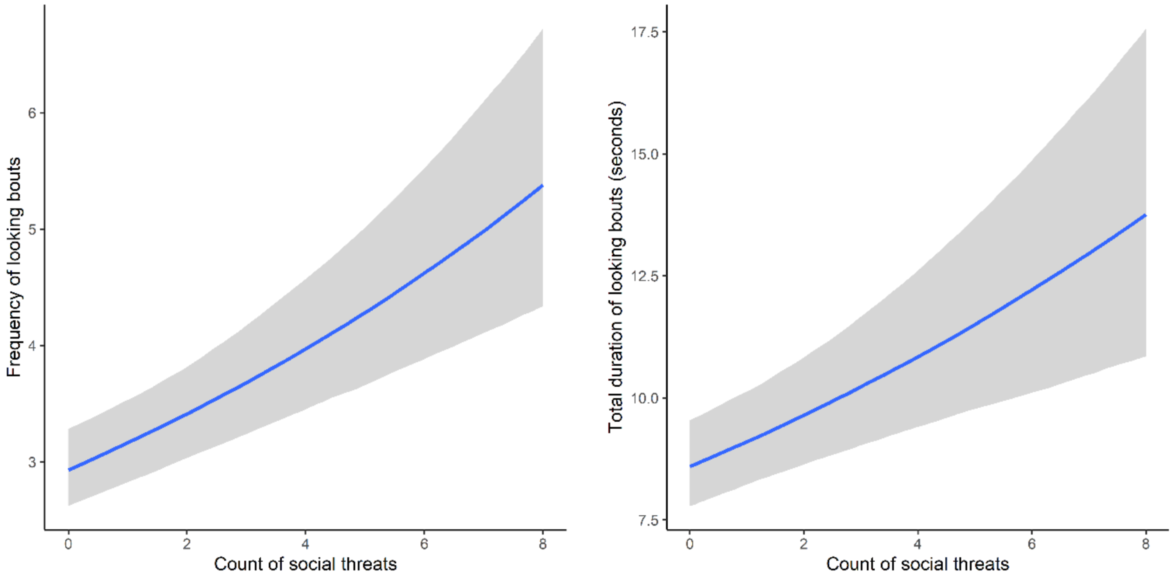

Figure 4. Conditional effects plots displaying the relationship between the number of social threats within 5 meters and the frequency and total duration of looking bouts. Shaded areas display the relevant credible intervals (2.5% and 97.5% quantiles).

Preemptive risk (models 16, 18, and 20) and observer-effects (model 21)

Models exploring the effect of leopard risk (model 16: leopard RSF), home range familiarity (model 18: IUD), and spatial risk of encountering another group (model 20: SEG) held zero weight for frequency models. The leopard model also held zero weight for the duration model, whilst the IUD and SEG models held minimal weight in the initial stacks. IUD held zero weight in the second stack whilst SEG continued to hold minimal weight relative to other models. The models exploring the interaction between individual tolerance scores and observer behaviours on looking patterns (model 21) also exhibited poor predictive accuracy. The frequency model produced minimal weight in the initial stack and 0 weight in the second stack, whilst the duration model shared no weight in either stack; suggesting observers were not a consistent nor significant driver of focal animal's looking patterns. The full summary results for these models (see supplementary material tables S14-15, S18-S19, S22-23, and S24-25) highlight some small trends do exist between certain interactive risk factors; however, the poor predictive performance of these models renders conclusions based on these results unreliable as the models are unlikely to predict more than a few observations with accuracy.

Habitat type (model 17)

Habitat models held a consistent, but low relative weight for the duration response variable, suggesting the habitat model may predict a small number of points with precision. This is likely true also for the frequency variable given the habitat model's relative weight was greater than 0.1 in the initial stack but held 0 weight in the second stack. Although it is unlikely that habitat type and its interactions with behaviour, spatial position, and number of neighbours are consistent drivers of looking behaviours in this group, some small effects can be elucidated which both support and oppose certain vigilance hypotheses (see figure 5). Full summary results for the frequency habitat model can be found in supplementary material (table S16).

Generally, the frequency of looking bouts was lower in forest and rock habitats, and highest on farms. Most habitats showed a clear positive interaction effect with time spent engaged. In particular, bush, grassland, rock, and woodland habitats were associated with more frequent bouts of looking when time spent engaged was low. Frequency of looking bouts were similar regardless of spatial position but was higher in peripheral locations (than central) when on farms and when animals were central in rocky areas. Finally, the interaction between number of neighbours and habitat types also produced a generally negative relationship with frequency of looking, i.e., frequency of looking decreased with increasing neighbours, however this was only substantive in grasslands where the mean conditional effect of 0 neighbours was higher than the upper credible intervals for 3 neighbours (and also for 3 neighbours versus 6 neighbours). Collectively, frequency of looking was relatively consistent across a range of scenarios.

The habitat model with a duration response variable produced a consistent but very low relative weight. This is likely explained by no specific interaction levels having a clear association with increased or decreased looking durations, see supplementary material (table S17 figs S7). For example, although time spent not engaged shared a strong positive association with looking duration in all habitats, the strength and direction of this association was consistent across all habitat types, rendering the interaction a poor predictor of looking patterns. Total duration of looking was also consistent across habitat types regardless of spatial position or number of neighbours (see fig S7).

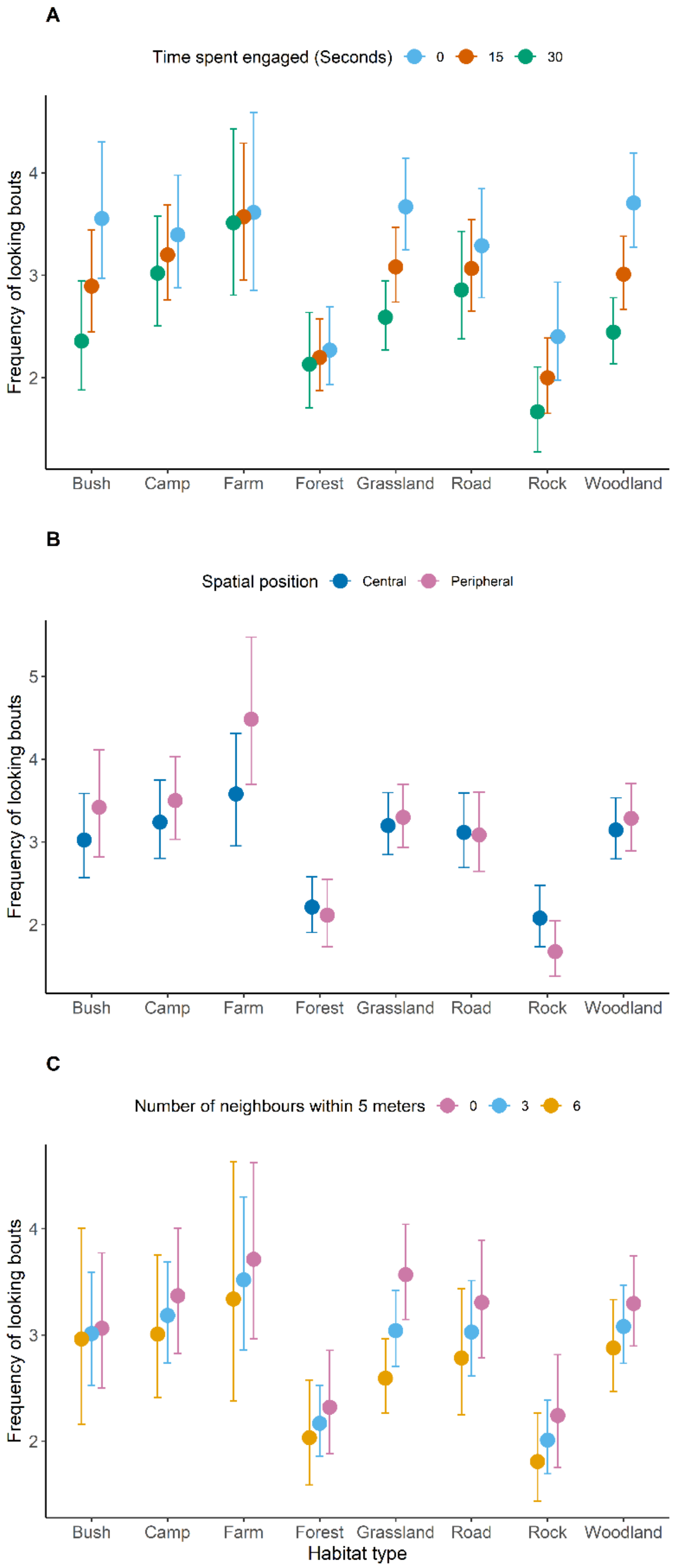

Figure 5. Conditional effects plots showing how the frequency of looking bouts varied according to the interaction between habitat type and (panel A) time spent engaged, (B) spatial position, and (C) number of neighbours within 5 meters. For time spent engaged the conditional means and credible intervals (2.5% and 97.5% quantiles) are shown for specific values of time spent engaged (i.e., 0, 15, 30 seconds) for graphical purposes only. This was also done for number of neighbours at different values (0, 3, and 6 neighbours).

Home-range familiarity – Core, frequently used, and boundary areas (model 19)

Home-range familiarity models using the categorical predictor (core, frequent, boundary, i.e., model 19) held weight in all stacks across both response variables. In particular, model 19 shared a weight above 0.1 for the frequency response variable before dropping to a negligible weight when stacks were simplified. The duration model held a consistently low weight regardless of the other models included in the stack. This again suggests that both models were able to predict certain values with greater accuracy than the other candidate models, although did not do so consistently. Full model results in supplementary material tables S20 and S21.

We observed a slight general trend for the frequency of looking bouts to increase with decreasing home range familiarity (see figure 6). Within core areas the frequency of looking bouts was lowest when time spent engaged was highest, with frequency increasing substantially as time spent engaged decreased. The same pattern was observed in frequently used and boundary areas, although the strength of the relationship was not as significant. We did not observe a clear trend to suggest that spatial position affected the frequency of looking bouts depending on home range familiarity. In contrast, we did find strong evidence that the frequency of looking bouts decreased with increasing neighbours in core and frequently used areas. Although we observed a similar trend in boundary areas, overlapping credible intervals suggested this effect was weak.

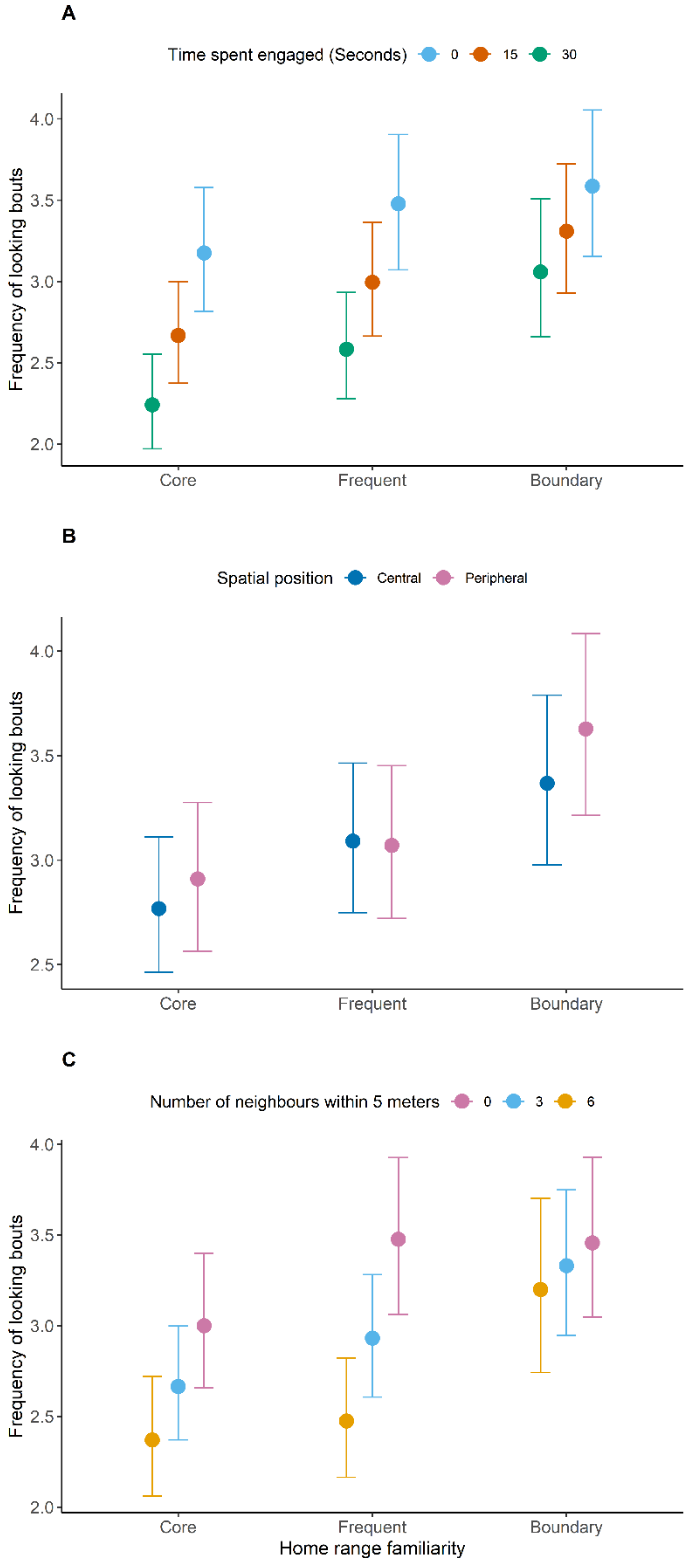

Figure 6. Conditional effects plots showing how the frequency of looking bouts varied according to the interaction between home range familiarity (core, frequently used, and boundary areas) and time spent engaged (panel A), spatial position (B), and number of neighbours within 5 meters (C). For time spent engaged the conditional means and credible intervals (2.5% and 97.5% quantiles) are shown for specific values of time spent engaged (i.e., 0, 15, 30 seconds) for graphical purposes only. This was also done for number of neighbours at different values (0, 3, and 6 neighbours).

Discussion

The majority of our observations were best explained by models incorporating information on specific behaviours and foraging task/intake rate. Despite these clear tendencies we still found that the total duration of looking bouts was higher whilst within-group conflict or encounters with other groups/foreign individuals were ongoing, indicative of reactionary vigilance use in both cases. The remaining reactionary models shared negligible weight across both response variables. Our preemptive risk models generally were assigned lower stacking weights, although we found some evidence for interactive effects within habitat and categorical home-range familiarity models. Both looking variables also shared a positive relationship with number of social threats within 5 meters, however, the predictive accuracy of these models was lower than behavioural and foraging models. There was also little evidence that observer proximity or movement influenced looking patterns, regardless of tolerance levels.

We predicted that biting and handling fruits or seed pods would allow for brief moments of compatible looking time and our results offer support for this (see table 3), as frequency of looking increased but duration of looking decreased as time spent biting and handling increased. This aligns well with previous findings that vigilance use shares some compatibility with food handling in mammals (59, 89, 90). We also found that items typically processed using their teeth (i.e., biting) were also associated with greater frequency of looking bouts. Digging, searching substrate, and picking (e.g., fruits, seeds, grass seeds etc.) time did not appear to influence the frequency of bouts substantially but each shared a strong negative relationship with the duration of looking. Additionally, duration of looking also held strong negative relationships with auto and allogrooming (giving), however, these behaviours did influence the frequency of looking bouts, this highlights the role engaged behaviours have in constraining when longer duration looking episodes can be performed.

When behaviours were grouped together into engaged or not engaged, we expected the total duration of looking behaviours to increase as time spent not engaged increased, and for the frequency of looking to increase with increased time spent engaged. The latter prediction was made as it has previously been shown that routine vigilance, i.e., brief movements (<1 second) of the head to monitor the surroundings, was higher during feeding than resting behaviours in ursine colobus monkeys (*Colobus vellerosus*) (61), highlighting that brief bouts can be used more frequently during engaged behaviours. However, for frequency models where time spent engaged was included as an additive effect, we found a negative relationship between time spent engaged and looking, which was also consistent in interaction models, e.g., the negative relationship was consistent across habitat types and categorical home range familiarity. These results reiterate that behaviours such as digging, picking, and grooming may require increased visual attention whilst offering little compatible looking time, even for brief glances. As frequency of looking did not increase during engaged behaviours according to preemptive risk scenarios, it suggests the baboons may not be risk-sensitive during these behaviours.

We also found no evidence that the interactions between preemptive risk factors (e.g., leopard RSF) and time spent not engaged were associated with consistent changes in the duration of looking, i.e., looking was consistently higher when time spent not engaged was high and this was not altered according to preemptive risk scenario. This is likely due to there being no inherent cost to looking when time spent not engaged (e.g., resting, chewing etc) is high (e.g., (15)). These relationships may also suggest that the baboons did not consistently avoid longer bouts of engaged behaviours as risk increased, and instead readily maximised looking whenever their underlying behaviour afforded opportunities to do so, e.g., when resting or chewing food.

Tasks such as digging and searching leaf litter for seeds take place exclusively on the ground, which forces baboons into a head down posture; as such, looking time is likely to hinder feeding rate or vice versa, e.g., (91). When leaves, grass blades, and grass seeds were the predominant food item the duration of looking was greater than all other items, including when no foraging or feeding behaviours took place (see figure 2). Leaves, grasses, and grass seeds were abundant in most food patches such that picking behaviours did not seem to require a precise focus of attention and an animal could look towards the next food item (i.e., promoting looking) whilst continuing to pick. Such tasks have numerous moments of compatible or cost-free looking time which can allow for looking without sacrificing foraging success significantly (15, 90). Even though these looking bouts may not be driven by risk, they likely still increase the likelihood of the animal detecting a threat if it was there, i.e., looking should share compatibility with threat detection (17, 92).

We previously found evidence that these study subjects were adept at detecting approaching threats (observers) rapidly if they were already looking around (but not towards the approacher), suggesting there should be compatibility between looking and threat detection. As such, the study animals are unlikely to be under significant pressure to use preemptive vigilance for external threats on a consistent basis, i.e., any driver that draws their visual attention beyond their hands and the substrate, object, or animal their hands are in contact with will increase their likelihood of detecting a localised threat if it is present. This may mean that a variety of visual search behaviours for non-threatening stimuli, e.g., food or mate search, communication with conspecifics, or route-planning, can achieve the function of preemptive vigilance and thus may explain why preemptive risk scenarios appear poor predictors of looking behaviours as we find here.

It has also been shown experimentally that animals undertaking complex foraging tasks have diminished threat detection capabilities (47); however, these study baboons were able to detect approaches made by observers quickly during engaged behaviours such as grooming or digging (see (48)). This may additionally suggest that these baboons can rely on acoustic cues to detect local threats during engaged behaviours, or alternatively, that none of the engaged tasks undertaken by these study animals are complex enough to diminish their sensory capacity, e.g., (47). The ability to still detect threats rapidly during engaged tasks may explain why we found little evidence that the baboons pre-emptively increased their looking behaviours in risky areas, as they can rely on their ability to detect threats regardless of behaviour. These results may be also be linked to them being in a large group where dilution and confusion effects are maximised, i.e., (7, 8, 93), and thus, individual risk perception (for external threats) may generally be quite low.

The positive association between foraging success (number of bites taken or number of items consumed) and the frequency of looking, and the negative relationship between foraging success and duration of looking could be interpreted a number of ways. Firstly, looking may be incompatible with feeding, thus an animal may diminish intake rate to invest more time in longer looking episodes (91). Alternatively, animals may prioritise feeding over longer looking episodes and therefore utilise shorter but more frequent bouts of looking to routinely update information on the surrounding environment (15). When food intake results are taken in combination with specific behavioural results there appears to be a strong suggestion that increased intake rate is associated with compatible looking time for many foraging tasks and feeding behaviours. As such, although longer duration looking episodes are less likely as foraging success increases, the compatible looking time during biting, handling, and some picking tasks offsets this reduction. These results suggest the baboons have a consistent tendency to utilise the compatible and cost-free moments of their underlying behaviours to update their information on the environment, but these moments do not appear correlated with preemptive risk scenarios.

Given that specific behaviours and foraging success/items models consistently predicted looking behaviours with greater accuracy than numerous risky scenarios, we suggest that engaging in preemptive vigilance for most external threats may often be unnecessary for this study group. We did however find that study animals looked around more frequently on farms when in peripheral locations, suggestive of preemptive vigilance for anthropogenic threats. Frequency of looking decreased with increasing time spent engaged in woodland and bush habitats and was consistently lowest in forest habitats regardless of behaviour. Given that areas with greater plant biomass (i.e., NDVI higher in forests than grasslands) were associated with greater probability of encountering a leopard (67), these results were counter to vigilance predictions.

Frequency of looking and time spent engaged also shared a negative relationship in rocky and grassland habitats, whilst there was a strong negative relationship between number of neighbours and frequency of looking in grassland habitats. Frequency of looking was also higher in the central spatial position in rocky habitats. Visibility did not share a significant relationship with frequency of looking, however, it shared a strong positive association with the duration of looking behaviours in all models. Together these results may suggest support for the protective cover hypothesis (25), i.e., animals increase preemptive vigilance use when in exposed areas; however, it may also suggest animals utilise enhanced visibility to collect personal or social/public information on a range of factors in these places (94).

The models specifically exploring the interaction between spatial position and cohesion garnered no weight in any of the stacks, again suggesting that broad risk dilution and confusion hypotheses (i.e., (7, 8, 93)) also do not explain looking behaviours in this group. However, in both core and frequently used areas, frequency of looking shared a strong negative relationship with number of neighbours. However, frequency was consistent across different number of neighbours in boundary areas, but there was also a general trend for frequency of looking to increase with decreasing home range familiarity. This may suggest that the study group perceive greater risk when cohesion is low, but only in familiar areas. When in boundary areas risk may be much higher (e.g., (30)) and therefore animals consistently increase the frequency of looking regardless of group cohesion, such trends may be indicative of preemptive vigilance for external threats. These results offer insights into the complexity of decision making and risk perception in wild animals; however, given the low weighting of habitat familiarity models and the scale of the effect sizes (see fig 6) it is unlikely these factors are consistent drivers of looking behaviours in this group; however, this is likely also driven by utilisation of boundary areas being much less common.

We found little evidence that looking patterns were altered according to spatial risk of encountering leopards or other groups, nor the proximity or behaviour of observers, regardless of tolerance levels, counter to findings supporting landscape of risk findings elsewhere (see (28)) and in this group (see (66). The contrasting results to the latter study is intriguing and suggests that methodological consistencies are clearly needed when making comparisons (95), even within the same study group. Despite not attempting to sample vigilance specifically we still identified reactionary vigilance use during periods of increased within-group conflict and encounters with other groups/foreign individuals. Interestingly, in both cases the animals returned to baseline levels of looking within 5 minutes, suggesting vigilance use may often be a more induced behaviour in this group (15), and that if a threat is worth monitoring the animals typically focus on it entirely.

Count of social threats within 5 meters was the only risk variable to produce the same direction (positive) relationship across both response variables. This supports social vigilance hypotheses which are also well supported across primate vigilance research (21, 31, 56, 57, 64, 65, 74). It should also be noted that social threat models did not yield any weight in the simplified stacks, suggestive of lower predictive accuracy than the specific behaviours and foraging success/items models. It is likely that the within-group threats model is good at predicting looking patterns when the number of threats is high but does poorly when they are absent. In addition, animals may avoid spending considerable time sharing space with within-group threats (96), and therefore may represent a low proportion of an animal's overall activity budget, and would therefore also contribute to poorer predictions of general looking behaviours.

To conclude, our analysis offers support for several popular vigilance hypotheses. Despite not attempting to sample vigilance specifically, we still identified that longer durations of reactionary vigilance were used during periods of increased within-group conflict and encounters with other groups/foreign individuals. In addition, our framework also identified trends for preemptive vigilance use in certain risky scenarios, e.g., being on the edge of the group on farms. However, weighting of the independent hypothetical models revealed that models investigating the role of specific behaviours and foraging success/items consistently predicted looking patterns with the highest degree of accuracy. As such, although vigilance had a clear role in certain reactionary circumstances, preemptive vigilance was clearly not a consistent functional determinant of this group's looking behaviours. Instead, results indicated that baboons may rely on the compatibility their natural behaviours have with looking and their capacity to collect multiple types of information concurrently to detect threats. If this is the case it could mean that any factor that encourages looking will increase the likelihood of the baboon's detecting a threat early, i.e., searching for food may reveal a predator if it was there (92).

Understanding the sensory capacity and threat detection capabilities of study animals should therefore be a topic for future research to explore in more detail as there is likely a differential need for preemptive vigilance across species with varying detective abilities. Given the relationships we found for specific behaviours, there's a strong possibility that risk sensitivities may be very nuanced and therefore require these questions to be explored on finer scales. For example, future work could break down foraging behaviours into the specific components used in this study (e.g., biting, digging, handling) and explore risk sensitivities within each specific behavioural bout. Such an approach would build a more complete picture of the compatible looking time various species have according to the behaviours and tasks they engage in, and how such factors vary temporally, i.e., different seasons offer different foraging tasks.

It could be argued that research can adequately sample the various subcomponents of vigilance directly, e.g., routine/induced (61), preemptive/reactionary (52); however, there is very little empirical evidence that researchers are able to do this task flawlessly, and the subject area requires urgent attention. Our previous work found that different vigilance definitions can lead to different results, whilst definitions also vary in how consistently they are interpreted by different observers (95). It seems likely definitions requiring observers to identify an animal's subject of gaze or internal state are likely to increase the likelihood of interpretational effects. We presented the looking definition and framework as a way to alleviate such issues (see (17) and found support that it can minimise definitional and interpretational effects in vigilance studies. A major criticism of our approach may have been that it makes no attempt to sample vigilance specifically; however, the results of this study give support to the notion that risk sensitive behaviours and their drivers can still be identified when using a broad definition and framework. We therefore encourage future work to consider exploring similar designs, especially as it may improve the reliability of inter-study comparisons (95).

References

1. G. Beauchamp, *Animal vigilance: monitoring predators and competitors* (Academic Press, 2015).
2. T. Caraco, Time budgeting and group size: a test of theory. *Ecology* **60**, 618–627 (1979).
3. H. R. Pulliam, On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422 (1973).
4. A. Treves, Within-group vigilance in red colobus and redtail monkeys. *Am. J. Primatol.* **48**, 113–126 (1999).
5. I. Krams, Dominance-specific vigilance in the Great Tit. *J. Avian Biol.* **29**, 55–60 (1998).
6. G. Roberts, Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086 (1996).
7. I. Vine, Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* **30**, 405–422 (1971).
8. W. D. Hamilton, Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311 (1971).
9. M. Milinski, R. Heller, Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus L.*). *Nature* **275**, 642–644 (1978).
10. G. F. Turner, T. J. Pitcher, Attack abatement: A model for group protection by combined avoidance and dilution. *Am. Nat.* **128**, 228–240 (1986).
11. M. Treisman, Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Anim. Behav.* **23**, 779–800 (1975).
12. A. J. Inman, J. Krebs, Predation and group living. *Trends Ecol. Evol.* **2**, 31–32 (1987).
13. K. M. Jack, Effect of Male Emigration on the Vigilance Behavior of Coresident Males in White-faced Capuchins (*Cebus capucinus*). *Int. J. Primatol.* **22**, 715–732 (2001).
14. F.-R. Favreau, A. W. Goldizen, O. Pays, Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proc. R. Soc. B* **277**, 2089–2095 (2010).
15. P. Blanchard, H. Fritz, Induced or routine vigilance while foraging. *Oikos* **116**, 1603–1608 (2007).
16. G. Beauchamp, What can vigilance tell us about fear? *Anim. Sentience* **2017.015**, 1–53 (2017).
17. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).
18. S. Creel, P. Schuette, D. Christianson, Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.* **25**, 773–784 (2014).
19. K. Ota, Fight, fatigue and flight: Narrowing of attention to a threat compensates for decreased anti-predator vigilance. *J. Exp. Biol.* **221** (2018).
20. A. Treves, Vigilance and Spatial Cohesion among Blue Monkeys. *Folia Primatol.* **70**, 291–294 (1999).
21. N. Kutsukake, Conspecific influences on vigilance behavior in wild chimpanzees. *Int. J. Primatol.* **28**, 907–918 (2007).
22. E. Fernández-Juricic, G. Beauchamp, An experimental analysis of spatial position effects on foraging and vigilance in brown-headed cowbird flocks. *Ethology* **114**, 105–114 (2008).

23. M. Öst, K. Jaatinen, B. Steele, Aggressive females seize central positions and show increased vigilance in brood-rearing coalitions of eiders. *Anim. Behav.* **73**, 239–247 (2007).

24. P. A. Bednekoff, D. T. Blumstein, Peripheral obstructions influence marmot vigilance : integrating observational and experimental results. *Behav. Ecol.* **20**, 1111–1117 (2009).

25. S. L. Lima, Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol.* **124**, 303–316 (1987).

26. G. Cowlishaw, The role of vigilance in the survival and reproductive strategies of Desert Baboons. *Behaviour* **135**, 431–452 (1998).

27. R. A. Fuller, S. Bearhop, N. B. Metcalfe, T. Piersma, The effect of group size on vigilance in Ruddy Turnstones Arenaria interpres varies with foraging habitat. 246–257 (2013).

28. F. A. Campos, L. M. Fedigan, Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behav. Ecol.* **25**, 477–486 (2014).

29. R. Steenbeek, R. C. Piek, M. van Buul, J. A. R. A. M. van Hooff, Vigilance in wild Thomas's langurs (*Presbytis thomasi*): The importance of infanticide risk. *Behav. Ecol. Sociobiol.* **45**, 137–150 (1999).

30. L. Busia, C. M. Schaffner, F. Aureli, Watch out or relax: conspecifics affect vigilance in wild spider monkeys (*Ateles geoffroyi*). *Behaviour* **153**, 107–124 (2016).

31. N. L. McNelis, S. L. Boatright-Horowitz, Social monitoring in a primate group: The relationship between visual attention and hierarchical ranks. *Anim. Cogn.* **1**, 65–69 (1998).

32. E. Z. Cameron, J. T. Du Toit, Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Anim. Behav.* **69**, 1337–1344 (2005).

33. S. L. Lima, Initiation and Termination of Daily Feeding in Dark-Eyed Juncos: Influences of Predation Risk and Energy Reserves. *Oikos* **53**, 3–11 (1988).

34. J. Burger, M. Gochfeld, Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. *Environ. Conserv.* **25**, 13–21 (1998).

35. F. Brivio, S. Grignolio, A. Brambilla, M. Apollonio, Intra-sexual variability in feeding behaviour of a mountain ungulate : size matters. 1649–1660 (2014).

36. R. Monclus, H. G. Rodel, Influence of Different Individual Traits on Vigilance Behaviour in European Rabbits. *Ethology* **115**, 758–766 (2009).

37. L. Barrett, J. O. Halliday, S. P. Henzi, The ecology of motherhood: the structuring of lactation costs by chacma baboons. *J. Anim. Ecol.* **75**, 875–886 (2006).

38. J. Lazarus, I. R. Inglis, The Breeding Behaviour of the Pink-Footed Goose: Parental Care and Vigilant Behaviour during the Fledging Period. *Behaviour* **65**, 62–88 (1978).

39. Z. Li, Z. Jiang, G. Beauchamp, Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *J. Zool.* **277**, 302–308 (2009).

40. A. Treves, A. Drescher, C. T. Snowdon, Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology* **109**, 135–146 (2003).

41. K. Onishi, M. Nakamichi, Maternal Infant Monitoring in a Free-ranging Group of Japanese Macaques (*Macaca fuscata*). *Int. J. Primatol.* **32**, 209–222 (2011).

42. M. Baldellou, P. S. Henzi, Vigilance, predator detection and the presence of supernumerary

males in vervet monkey troops. *Anim. Behav.* **43**, 451–461 (1992).

43. J. Burger, M. Gochfeld, Effects of group size and sex on vigilance in ostriches (*Stuthio camelus*): Antipredator strategy or mate competition? *Ostrich J. African Ornithol.* **59**, 14–20 (1988).

44. K. Nowak, A. Le Roux, S. A. Richards, C. P. J. Scheijen, R. A. Hill, Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* **25**, 1199–1204 (2014).

45. G. Beauchamp, Antipredator vigilance decreases with food density in staging flocks of Semipalmated Sandpipers (*Calidris pusilla*). *Can. J. Zool.* **92**, 785–788 (2014).

46. P. A. Bednekoff, S. L. Lima, Testing for peripheral vigilance: Do birds value what they see when not overtly vigilant? *Anim. Behav.* **69**, 1165–1171 (2005).

47. U. Kaby, J. Lind, What limits predator detection in blue tits (*Parus caeruleus*): Posture, task or orientation? *Behav. Ecol. Sociobiol.* **54**, 534–538 (2003).

48. A. T. L. Allan, A. L. Bailey, R. A. Hill, Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Sci. Adv.* **6**, eaaz0870 (2020).

49. G. Beauchamp, Function and structure of vigilance in a gregarious species exposed to threats from predators and conspecifics. *Anim. Behav.* **116**, 195–201 (2016).

50. K. P. Burnham, D. R. Anderson, K. P. Huyvaert, AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35 (2011).

51. Y. Yao, A. Vehtari, D. Simpson, A. Gelman, Using Stacking to Average Bayesian Predictive Distributions (with Discussion). *Bayesian Anal.* **13**, 917–1007 (2018).

52. S. U. E. Boinski, *et al.*, Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis, S. sciureus*). *Behaviour* **139**, 1421–1467 (2003).

53. D. Fragaszy, Sex and age differences in the organisation of behaviour in wedge-capped capuchins, *Cebus olivaceus*. *Behav. Ecol.* **1**, 81–94 (1990).

54. A. D. Gosselin-Ildari, A. Koenig, The Effects of Group Size and Reproductive Status on Vigilance in Captive *Callithrix jacchus*. *Am. J. Primatol.* **74**, 613–621 (2012).

55. A. Treves, A. Drescher, N. Ingrisano, Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behav. Ecol. Sociobiol.* **50**, 90–95 (2001).

56. K. M. Gaynor, M. Cords, Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Anim. Behav.* **84**, 531–537 (2012).

57. N. Kutsukake, The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology* **112**, 581–591 (2006).

58. M. Cords, Predator Vigilance Costs of Allogrooming in Wild Blue Monkeys. *Behaviour* **132**, 559–569 (1995).

59. G. Cowlishaw, *et al.*, A simple rule for the costs of vigilance: empirical evidence from a social forager. *Proc. R. Soc. B Biol. Sci.* **271**, 27–33 (2004).

60. K. R. L. Hall, Numerical Data, Maintenance Activities and Locomotion of the Wild Chacma Baboon, Papio Ursinus. *Proc. Zool. Soc. London* **139**, 181–220 (1962).

61. J. A. Teichroeb, P. Sicotte, Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behav. Ecol. Sociobiol.* **66**, 453–466 (2012).

62. A. Treves, Theory and method in studies of vigilance and aggregation. *Anim. Behav.* **60**, 711–722 (2000).

63. M. Suzuki, H. Sugiura, Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. *Am. J. Primatol.* **73**, 623–631 (2011).

64. D. P. Watts, A preliminary study of selective visual attention in female mountain gorillas (*Gorilla gorilla beringei*). *Primates* **39**, 71–78 (1998).

65. P. L. Pannozzo, K. A. Phillips, M. E. Haas, E. M. Mintz, Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (*Cebus apella*). *Ethology* **113**, 881–888 (2007).

66. A. M. Ayers, A. T. L. Allan, R. A. Hill, Foraging in fear: spatial variation in range use, vigilance, and perceived risk in chacma baboons (*Papio ursinus*). *Rev.*

67. A. M. Ayers, "The behavioural ecology and predator-prey interactions of leopards (Panthera pardus) and chacma baboons (*Papio ursinus*) in an Afromontane environment," Durham University. (2019).

68. A. J. J. MacIntosh, P. Sicotte, Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): An examination of the effects of conspecific threat and predation. *Am. J. Primatol.* **71**, 919–927 (2009).

69. A. Treves, K. Brandon, "Tourist impacts on the behavior of black howler monkeys (*Alouatta pigra*) at Lamanai, Belize" in *Commensalism and Conflict: The Human-Primate Interface*, (2005), pp. 147–167.

70. A. T. L. Allan, R. A. Hill, A. L. Bailey, Flight and visual orientation distance remained consistent in a single group of habituated chacma baboons after an observed predation by a leopard. Do flight initiation distance methods always measure perceived predation risk? *Rev.*

71. A. T. L. Allan, A. White, R. A. Hill, Intolerant baboons avoid observer proximity, creating biased inter-individual association patterns. *Rev.*

72. N. G. Caine, S. L. Marra, Vigilance and social organization in two species of primates. *Anim. Behav.* **36**, 897–904 (1988).

73. R. H. Haude, J. G. Graber, A. G. Farres, Visual observing by rhesus monkeys: Some relationships with social dominance rank. *Anim. Learn. Behav.* **4**, 163–166 (1976).

74. E. B. Keverne, R. A. Leonard, D. M. Scruton, S. K. Young, Visual monitoring in social groups of talapoin monkeys (*Miopithecus talapoin*). *Anim. Behav.* **26**, 933–944 (1978).

75. B. T. Coleman, R. A. Hill, Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Anim. Behav.* **88**, 165–173 (2014).

76. E. P. Willems, R. A. Hill, Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology* **90**, 546–555 (2009).

77. S. T. Williams, K. S. Williams, B. P. Lewis, R. A. Hill, Population dynamics and threats to an apex predator outside protected areas: Implications for carnivore management. *R. Soc. Open Sci.* **4** (2017).

78. A. McVean, P. Haddlesey, Vigilance schedules among House Sparrows *Passer domesticus*. *Ibis (Lond. 1859).* **122**, 533–536 (1980).

79. J. P. Curley, compete: Analyzing Social Hierarchies: R package version 0.1 (2016).

80. G. Csardi, T. Nepusz, igraph. *InterJournal, Complex Syst.*, 1695 (2006).

81. A. J. Lyons, W. C. Turner, W. M. Getz, Home range plus: a space-time characterization of movement over real landscapes. *Mov. Ecol.* **1**, 2 (2013).

82. W. M. Getz, *et al.*, LoCoH: Nonparameteric Kernel methods for constructing home ranges and utilization distributions. *PLoS One* **2**, e207 (2007).

83. R. T. Pitman, *et al.*, Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. *J. Appl. Ecol.* **54**, 1687–1698 (2017).

84. P.-C. Bürkner, Package ‘ brms ’ (2019) https:/doi.org/10.32614/RJ-2018-017>.

85. P.-C. Bürkner, brms : An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

86. J. Gabry, D. Simpson, A. Vehtari, M. Betancourt, A. Gelman, Visualization in Bayesian workflow. *J. R. Stat. Soc. Ser. A Stat. Soc.* **182**, 389–402 (2019).

87. A. Vehtari, A. Gelman, J. Gabry, Y. Yao, loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. *R Packag. version 2.0.0* (2018).

88. A. Vehtari, D. P. Simpson, Y. Yao, A. Gelman, Limitations of “ Limitations of Bayesian Leave-one-out Cross-Validation for Model Selection .” *Comput. Brain Behav.* **2**, 22–27 (2019).

89. I. J. Makowska, D. L. Kramer, Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. *Anim. Behav.* **74**, 153–158 (2007).

90. D. Fortin, M. S. Boyce, E. H. Merrill, J. M. Fryxell, Foraging costs of vigilance in large mammalian herbivores. *Oikos* **107**, 172–180 (2004).

91. H. Fritz, M. Guillemain, D. Durant, The cost of vigilance for intake rate in the mallard (*Anas platyrhynchos*): An approach through foraging experiments. *Ethol. Ecol. Evol.* **14**, 91–97 (2002).

92. A. Treves, The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour* **135**, 453–481 (1998).

93. M. Milinski, A predator’s costs of overcoming the confusion-effect of swarming prey. *Anim. Behav.* **32**, 1157–1162 (1984).

94. E. Danchin, L. A. Giraldeau, T. J. Valone, R. H. Wagner, Public Information: From Nosy Neighbours to Cultural Evolution. *Am. Assoc. Adv. Sci.* **305**, 487–491 (2004).

95. A. T. L. Allan, R. A. Hill, Definition and interpretation effects: How different vigilance definitions can produce varied results. *Rev.*

96. C. H. Janson, Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Anim. Behav.* **40**, 922–934 (1990).

97. N. C. Bonnot, *et al.*, Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).

98. R Core Team, R: A language and environment for statistical computing. Version 3.6.1. *R Found. Stat. Comput. Vienna, Austria* (2019).

99. R. McElreath, *Statistical Rethinking 2: A Bayesian Course with Examples in R and Stan*, Second (2019).

100. T. M. Houslay, A. J. Wilson, Behavioral Ecology Avoiding the misuse of BLUP in behavioural ecology. *Behav. Ecol.* **28**, 948–952 (2017).

Supporting information

S1: Age-sex class categories and descriptions

Text S1. Age-sex class categories and descriptions

Female baboons:

Adult female – Attainment of full body size, either cycling regularly, pregnant or lactating. Nipples also enlarge and elongated from suckling infants.

Adult female with infant contact – Adult females with dependent infants (black pelage and natal/pink skin colouration) within immediate sight. In open areas with high visibility, this could extend upto 10 meters as long as the infant was not isolated/exposed, e.g., had other baboons within 5 meters or was playing with other infants or juveniles. In areas of dense vegetation, the adult female needed to have direct line of sight to her infant to be considered 'in contact', as such, infants were occasionally considered not in contact with their mothers despite being relatively close.

Adult female with infant OS (out of sight) – Adult females with dependent infants beyond their immediate sight. This could be infants obscured by dense vegetation, beyond 10 meters away, or between 5 and 10 meters but with no other individuals within 5 meters, i.e., exposed/isolated.

ADF (Adolescent Female) – Nearly adult female size, with the onset of the first sexual swellings. If visible, nipples are much smaller and button-like than that of an adult female.

Male baboons:

AM (Adult male) – All secondary sexual characteristics fully grown, musculature (most noticeably in chest and rump) expands to full adult size.

ADM (Adolescent Male) – Massive growth in secondary sexual characteristics; testes expand, canines and mane grow longer, body size increases to near that of an adult male.

J3M (Juvenile 3 Males Only) – Body size at least that of an adult female, muzzle further extended to nearly that of an adult male. Testes start to expand and are clearly visible. Mane becomes noticeable.

Juvenile baboons of both sexes:

J2M/F (Juvenile 2) – Little demarcation from previous period, with greater body size. Hair becomes darker, changing to a more adult grey/brown colouration.

J1M/F (Juvenile 1) – Little demarcation from infants, but fully weaned and nutritionally independent. Muzzle starts becoming more elongated and pronounced. Pelage is still lighter than in juvenile 2. Male/female distinction based on genitalia and noticeable absence/presence of a separation in the callosities.

S2: Methods for assessing visibility

Aim: To explore whether the observer (AA) could assess habitat visibility as a percentage for each focal observation.

To assess this aim, AA generated 20 random GPS locations within the baboon's core ranging area. At each GPS location horizontal habitat visibility was assessed in each cardinal and intercardinal (i.e., north-east, south-east, etc.,) direction to both 5 meter and 10-meter distances, each assessment was completed at both 50cm (to reflect baboon eye-level on the ground) and 1.5 meters (to reflect animal's foraging in trees). At each direction, distance, and height a photograph was taken (from the GPS location) towards a 1x1 meter checkerboard with 225 squares, generating 32 checkerboard photos for each GPS location. The number of squares visible in each photo was then counted post-hoc. For each plot, the percentage of visible squares was calculated as a percentage of total squares for cardinal and intercardinal directions separately, and for each height separately, producing a total of four visibility assessments for each plot (i.e., 50cm cardinal direction, 1.5m cardinal, 50cm intercardinal, 1.5m intercardinal), 80 assessments across all 20 plots.

At each plot AA would also visually assess visibility to 5 and 10 meters at 50cm and 1.5m from the ground, taking into account numerous visual obstructions that could hinder a baboon's view to those distances in a 360-degree view. To assess the validity of AA's assessments, the cardinal and intercardinal assessments were plotted along with a regression line calculated from a linear model exploring their relationship (see fig S1). The predictions intervals for the cardinal vs intercardinal relationship were then calculated at the 95% level and added to the plot to represent upper and lower prediction intervals, AA's visual assessments were then added. As figure S1 highlights, only two of AA's visual assessments were outside of the prediction interval calculated from checkboard assessments, suggesting that 97.5% of these assessments were within the prediction bounds. Although, there is a suggestion that the visual assessments may be very slightly higher than checkerboard assessments this may also be because the observer is able to incorporate more information than the four photographs taken in each direction.

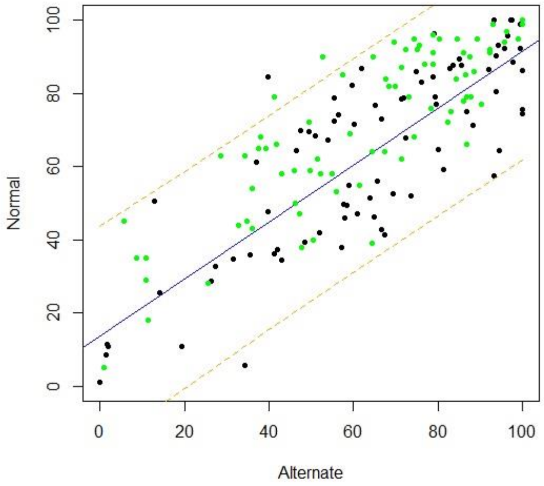

Figure S1. Regression between checkerboard visibility assessments of cardinal ('normal') direction and the alternate checkboard placements (intercardinal). Black dots represent the checkerboard visibility assessments, and the blue line is the linear model relationship between these assessments. The dashed orange lines represent the prediction intervals calculated at 95%. The green dots represent the visual assessments of the same locations by the observer, highlighting the observer's assessment fall within the prediction interval of the checkerboard assessments.

S3: Descriptions of habitat types

Text S2. Descriptions of the various habitat types categorised in this study

Habitat type – the Lajuma field site and surrounding properties contain a range of habitat types that can be broadly classified into several categories: forest, woodland, bush, camp, farm, grassland, and rocky areas. These habitat types vary in their respective structure and potential threats.

Forest: An area composed largely of trees with overlapping crowns forming 60-100% cover. Trees will be mostly tall providing extensive and near continuous shade.

Woodland: Canopy is more open than forest, with 25-60% cover, allowing sunlight to penetrate between the trees. Woodlands may support an understory of shrubs, herbs, or grasses.

Bush: An area where shrubs or are the dominant vegetation. A shrub is a woody perennial plant, smaller than a tree, with several major branches arising near the base of the stem. Areas of extensive tree regeneration, i.e., saplings, can also qualify as bush.

Grassland or savannah: Open area covered predominantly with grass. These areas may be devoid of trees entirely but can also contain widely spaced trees with a minimum of 5% cover to a maximum of 25% cover. Also included marshland which was exclusively found in flat regions along permanent water streams on peat. Vegetation components of marshlands include reeds, sedges, and grasses.

Rock: Areas where ground predominantly consists of rocks and boulders, rather than soil. Typically open and devoid of vegetation, as such, visibility can be higher in places, which can allow very distant threats to be detected.

Road: Dirt roads that run through the study area. Very little traffic (less than 5 vehicles a day) and always at low speeds (less than 10mph). Road use often offers a localised enhancement in visibility for the baboons.

Camp: Used or disused human settlements on Lajuma and neighbouring properties. Occasionally chased away from properties but usually very passive interactions with humans in these areas. Likely predation risk is lower, but conflict with domestic dogs is most common in these locations.

Farm: Ottosdal Macadamia farm or area around Ottosdal farmhouse, a consistent site for conflict with humans.

S4: Spatial risk layers for preemptive vigilance hypotheses

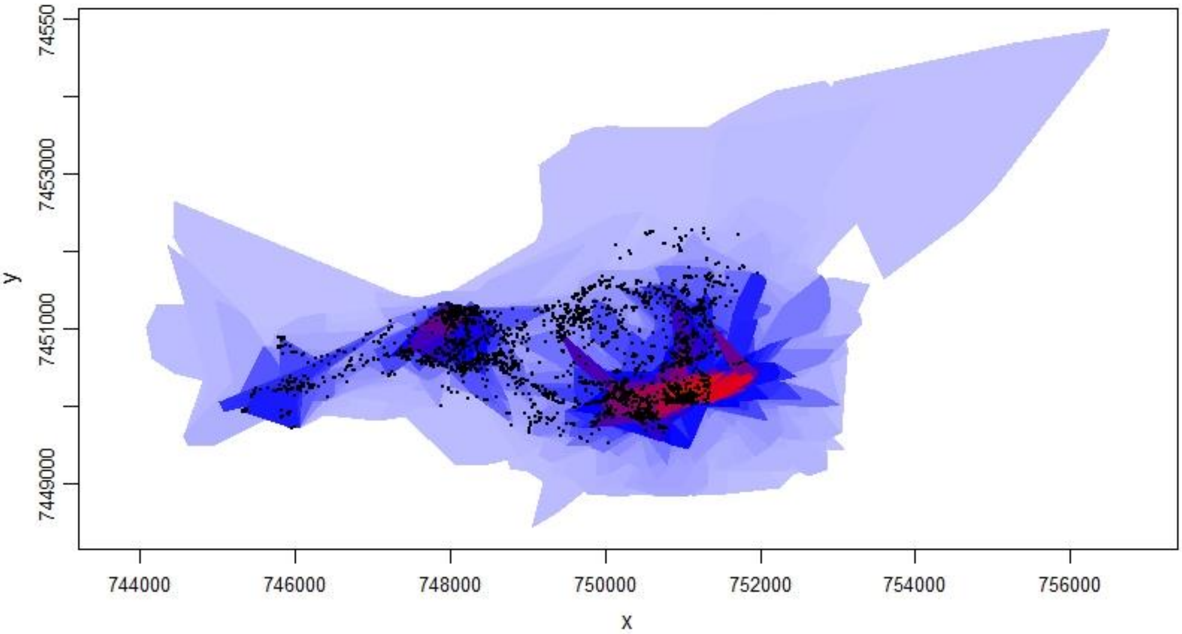

Figure S2. Utilisation distribution for study group calculated from GPS point collected at 20-minute intervals between 2015 and 2019. Light blue represents low use areas and red high-use areas. Black points are the distribution of focal observation used for the looking analysis.

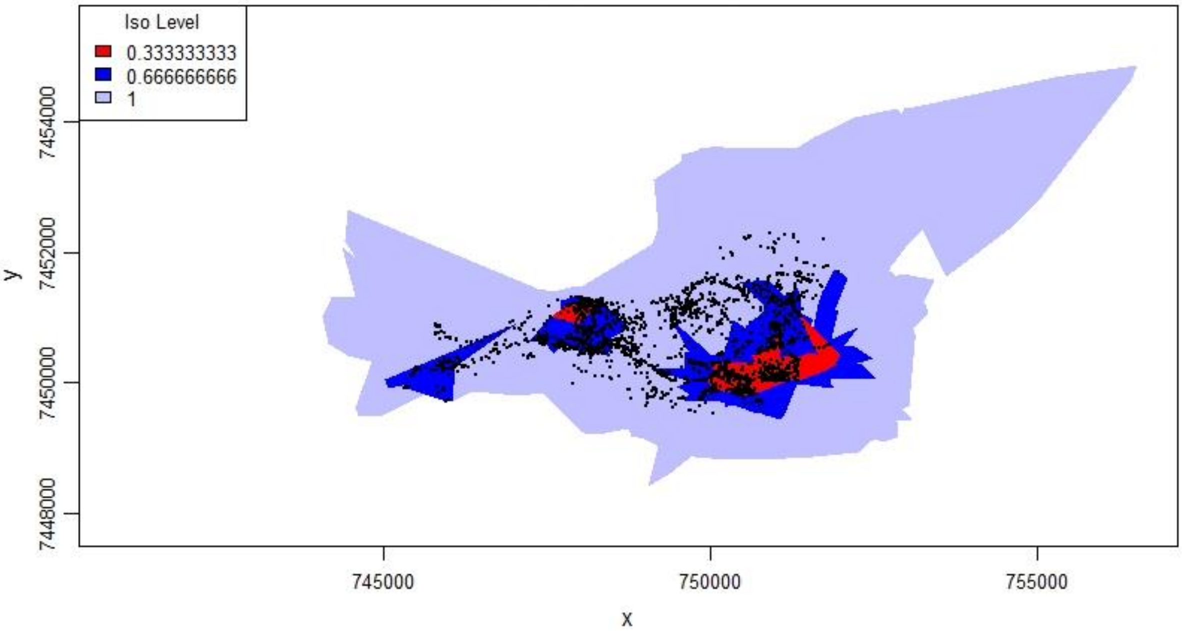

Figure S3. Utilisation distribution for study group calculated from GPS point collected at 20-minute intervals between 2015 and 2019. Light blue represents low use 'boundary' areas (iso level of 1), dark blue represent 'frequently' used areas (iso level of 0.6), and red represents high-use 'core' areas (iso level 0.3). Black points are the distribution of focal observation used for the looking analysis.

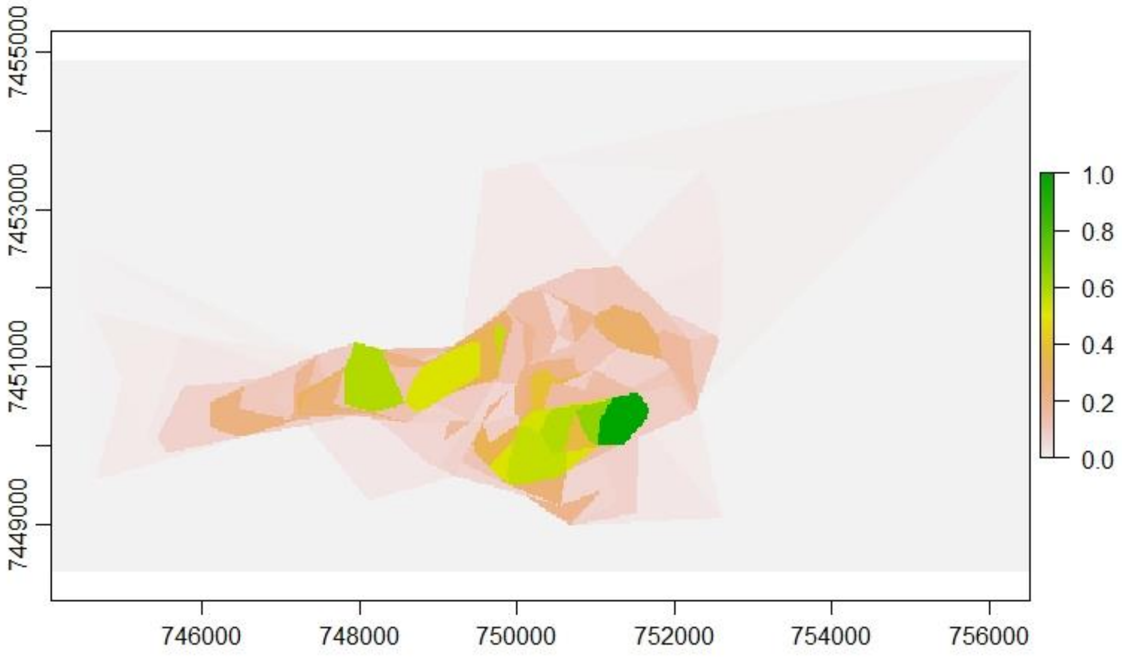

Fig S4. Scaled raster layer representing the distribution of observed encounters between the study group and other groups of baboons.

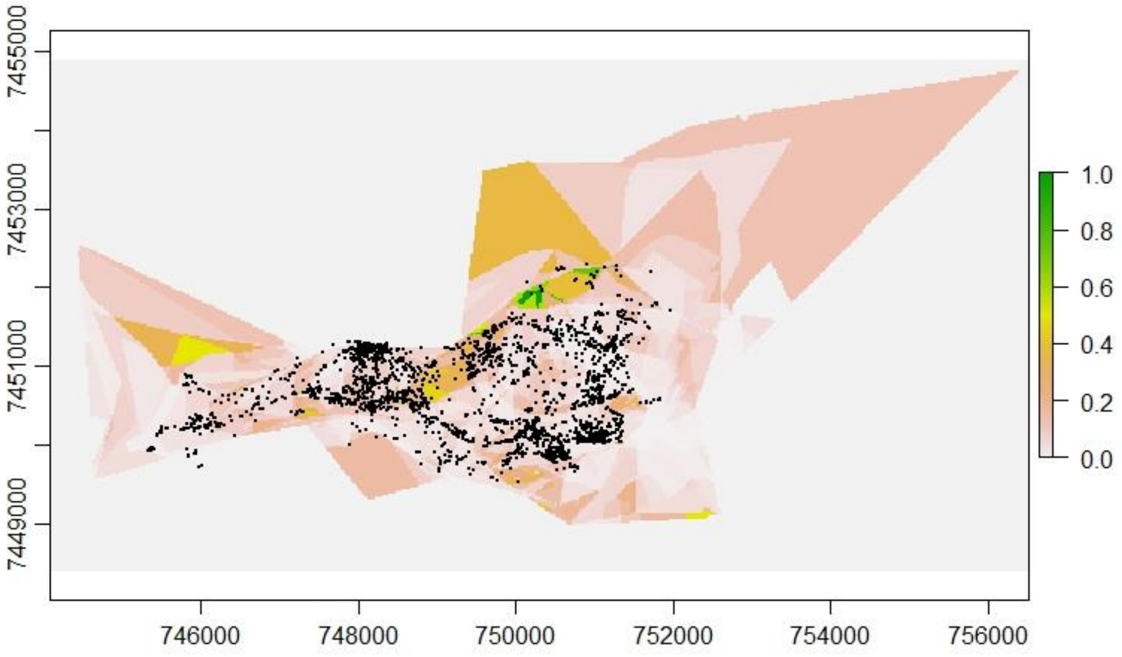

Fig S5. Scaled raster layer representing the probability of encountering another group. Scaled raster layer of distribution of observed encounters between the study group and other groups (Fig S4) divided by a raster of the scaled utilisation distribution (S2).

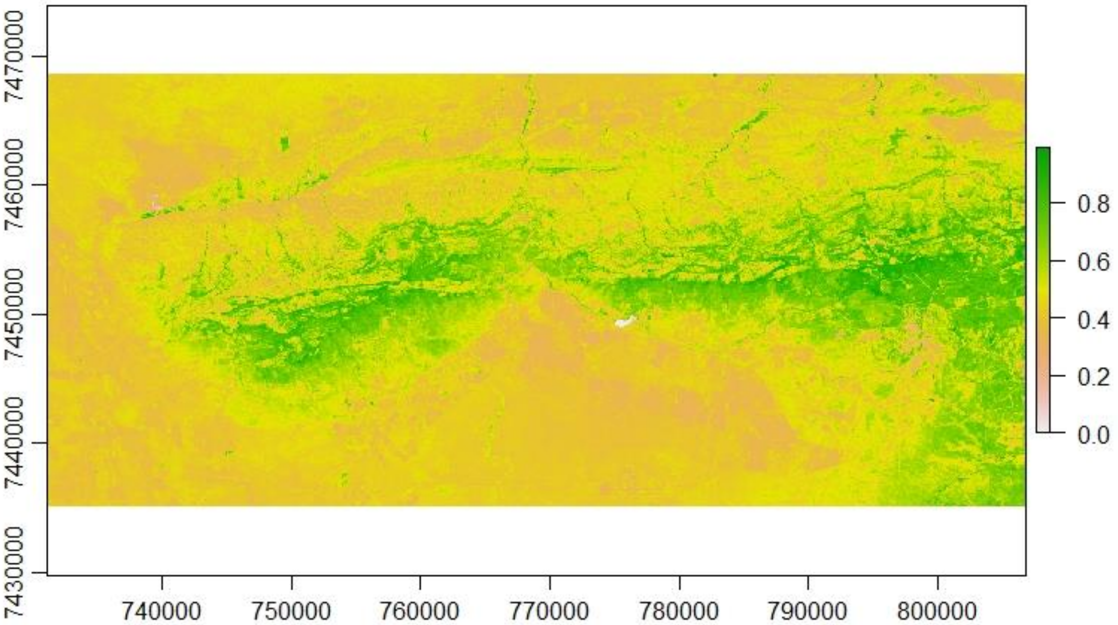

Fig S6. Scale integrated RSF calculated by multiplying each pixel from the 2nd order and 3rd order resource selection functions calculated by Ayers (2019).

S5: Calculating visual tolerance

Visual orientation distance (VOD) was previously found to be distinct amongst individuals and repeatable within each individual, evidence that visual tolerance may be an individual level trait (48). VOD remained consistent across individuals and the group regardless of whether the approaching observer was familiar or unfamiliar and we found no evidence of habituation or sensitization effects across any temporal level. Nevertheless, to additionally guard against these factors in this study, the model used to calculate visual tolerance estimates (i.e., conditional modes) was updated from (48) to include additional fixed effects that tracked individual trial number per day and group trial number across all individuals per day. We retained the observer identity and observer trial number interaction as both fixed effects and random slopes over individual identity. This interaction was integral to our study design and ensured habituation and sensitization effects were explored effectively across all temporal levels. We removed the fixed effects of neighbour flee first and external factors within 5 minutes from the models used in (48) as they were previously shown not to effect FID in a significant way and we did not want to over parameterize the updated model.

As with (48), the fixed effects of engaged, habitat, height, and number of neighbours within 5 meters were also retained as all were found to be important previously. Date was also included as a random effect crossed with individual identity. Visual orientation distance delay (the difference between start distance and VOD) was included as a fixed effect and random slope over individual identity to control for issues relating to the envelope constraint see (17, 97). In all cases, random slopes were modelled with correlated intercepts to ensure the estimated model captured all levels of by-individual variation. As this study was also focused on social factors inherent to each study animal, we also included dominance rank and age-sex class as fixed effects in the updated model, ensuring these elements of phenotypic variation were accounted for in the individual tolerance estimates (see Allan, White, Hill (In Rev)). Rank was calculated using the *isi13* function from the *compete* package (79), based on all displacement, supplant, and agonistic dyadic events between April 2017 and April 2018 (n=908), fights between males were excluded as the 'winner' can often be subjective during conflict. Age-sex class was defined according to secondary sexual characteristics (e.g., testes descending/enlarging, sexual swelling, canine eruption) and changes in pelage throughout juvenile development (see supporting information text S2 for full descriptions).

The updated model was fit using the *brm* function from the *brms* package (85) in the R software (98). Each model was run for six Hamiltonian Markov chains for 15000 iterations, warmup iterations were set to 5000 and adapt_delta to 0.95. All these parameters were set higher than default to allow algorithms to converge efficiently, producing robust posterior samples (85, 99). The model was fit with a Log-normal response distribution and default link function. The Gelman-Rubin convergence diagnostic (Rhat) was equal to 1 in all cases, strongly suggesting accuracy of the response variable to the Log-normal response distribution, i.e., the standard deviation of occurrence points formed around the Log-normal function was minimal. Normal priors (mean = 0, standard deviation = 100) were assigned for population (i.e., fixed) effects within the brm function; the remaining model components were assigned default Student *t* priors (df = 3, mean = 0, scaling factor = 10), apart from the standard deviations of the group-level effects which were constrained to be positive and therefore used a half Student-t prior with the same df, mean, and scaling factor. We compared our observed data to data simulated from the posterior predictive distribution of our models using the pp_check function and were confident our models were able to accurately predict our observed data.

Table S1. Updated visual orientation distance model results

Population-level effects							
	Estimate	Est.Error	L-95% CI	U-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	1.32	0.2	0.93	1.72	1	21442	33547
VODD	-0.01	0.01	-0.03	0.01	1	41824	44013
Compatibility (Looking)	0.21	0.02	0.17	0.24	1	82948	46341
Compatibility (Not engaged not looking)	0.11	0.02	0.06	0.16	1	87181	48336
Open (Habitat)	0.16	0.02	0.12	0.19	1	93579	44814
Ground (Height)	0.04	0.05	-0.05	0.14	1	91190	48336
Number of neighours	-0.04	0.01	-0.06	-0.03	1	99690	46290
Unfamiliar observer (AB)	-0.24	0.14	-0.52	0.05	1	25433	34299
Individual trial number per observer	0	0.01	-0.02	0.02	1	37100	42669
Group trial number per observation day	-0.01	0	-0.02	0	1	29037	38175
Individual trial number per observation day	0	0.03	-0.05	0.05	1	91368	47158
Dominance rank	0	0	0	0	1	28745	38582
Adolescent males	-0.1	0.15	-0.39	0.18	1	16437	31676
Adolescent females	0.14	0.09	-0.04	0.33	1	14228	26204
Adult females with infants	0.23	0.09	0.04	0.41	1	15390	27741
Adult males	0.15	0.13	-0.11	0.41	1	15639	26900
Juvenile females (J1F)	-0.03	0.12	-0.27	0.21	1	17193	28360
Juvenile males (J1M)	-0.16	0.11	-0.38	0.06	1	13976	28095
Juvenile females (J2F)	-0.06	0.12	-0.29	0.18	1	18648	30249
Juvenile males (J2M)	-0.12	0.12	-0.35	0.11	1	13541	27141
Juvenile males (J3M)	-0.04	0.12	-0.29	0.2	1	14379	28584
Unfamiliar observer (AB) : Trial number per observer	0.01	0.01	-0.01	0.03	1	27018	37502
Family specific (log-normal)							
Sigma	0.31	0.01	0.3	0.32	1.00	56100	43987
Group-level effects							
Date (58 levels)							
sd(Intercept)	0.1	0.01	0.07	0.13	1.00	17429	31353
Individual identity (69 levels)							
sd(Intercept)	0.18	0.03	0.13	0.25	1.00	18997	32193
sd(VODD)	0.04	0.01	0.03	0.06	1.00	27578	37332
sd(ObserverAB)	0.1	0.04	0.01	0.17	1.00	11854	13081
sd(TrialNo)	0.01	0	0	0.02	1.00	10034	23981
sd(ObserverAB:TrialNo)	0.01	0.01	0	0.02	1.00	7128	18929
cor(Intercept,VODD)	0.6	0.2	0.16	0.91	1.00	15412	27619
cor(Intercept,ObserverAB)	0.33	0.29	-0.3	0.82	1.00	24189	32547
cor(VODD,ObserverAB)	0.25	0.3	-0.39	0.76	1.00	27606	34331
cor(Intercept,TrialNo)	-0.45	0.34	-0.89	0.41	1.00	21043	35075
cor(VODD,TrialNo)	-0.17	0.34	-0.77	0.56	1.00	33161	41968
cor(ObserverAB,TrialNo)	-0.14	0.37	-0.79	0.61	1.00	34430	45452
cor(Intercept,ObserverAB:TrialNo)	0.2	0.34	-0.53	0.77	1.00	24616	35985
cor(VODD,ObserverAB:TrialNo)	0.19	0.33	-0.52	0.76	1.00	39174	37550

cor(ObserverAB,ObserverAB:TrialNo)	-0.03	0.39	-0.71	0.73	1.00	24440	38864
cor(TrialNo,ObserverAB:TrialNo)	-0.29	0.4	-0.88	0.6	1.00	12224	32548

We found no evidence that the study subjects habituated or sensitized across any timeframe as a result of the approaches completed previously. Ongoing monitoring of study subject's behavioural responses also validated this (see (48)), providing strong evidence that the methods did not create stress or anxiety in the study subjects. We also found no evidence that dominance rank was a driver of VOD (estimate 0 with upper and lower 95% upper credible intervals both at zero). Most age-sex classes had credible intervals that included zero, suggesting little confidence that age-sex class clearly drove visual orientation distance (see fig S6). However, adult males and females visually oriented slightly quicker than the younger individuals, with adult females with infants having the highest mean conditional effect, however, this may be expected as adult females with infants are likely to be the most risk sensitive animals whilst adult males can include individuals who immigrated from surrounding non-habituated groups, thus their individual tolerances were lower.

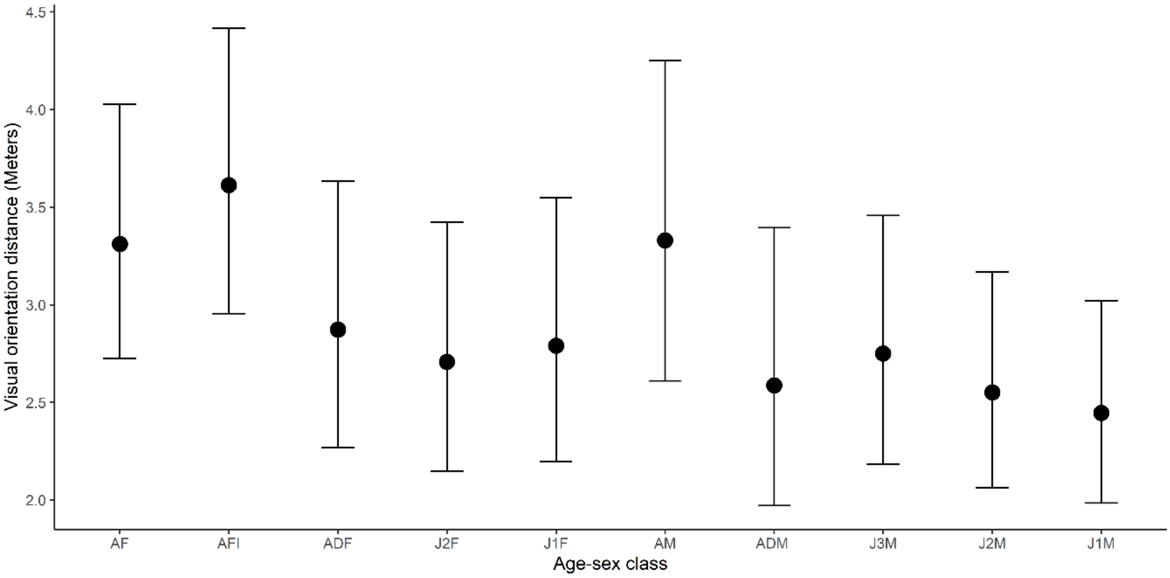

Fig S6. Conditional effects plot for each age-sex class and flight initiation distance. The mean was used as the measure of central tendency, 2.5 and 97.5% percent credible intervals also displayed. From left to right on the x-axis: adult females, adult females with infant, adolescent females, juvenile-2 females, juvenile-1 females, adult males, adolescent males, juvenile-3 males, juvenile-2 males, and juvenile-1 males (see text S2 for descriptions).

The intraclass correlation coefficient (ICC) for the updated model was slightly lower (updated individual identity ICC: 0.26; highest density intervals (HDI) for posterior samples at 95% intervals, 0.14, 0.39) compared to the findings reported in (48) (ICC, 0.38; HDI, 0.24,0.51). ICC estimates the ratio of the variance associated with individual identity effect divided by the total variance, i.e., sum of individual and residual variances, ($VAR_{ind}/VAR_{ind} + VAR_{resid}$), and therefore informs researchers of the degree of variance explained by individual differences, i.e., individual consistency (100).

The sum of individual variances for the updated model was (2113.874) far lower than the sum of the individual variances from the original model (3592.26), suggesting the updated model explained less individual level variance than the previous model. The higher sum of residual variances in the updated model (5758.474) compared to the original model (5751.353) also suggests that the unexplained variance is lower in the original model compared to the updated one. As a result of these factors the ICC equation produces a lower value for the updated model. Regardless of the decrease in ICC estimate, the HDI parameter values did not include zero, suggesting there was still moderate evidence for repeatability of VOD.

We then extracted the individual conditional modes from the updated model using the *ranef* function in *brms* and performed a Pearson's correlation between the conditional modes from the updated model and the conditional modes from the previous article. Individual tolerance estimates were consistent (r(67) = .876, p < .001) despite the changes in model structure from (48). As such, given the similarity in the conditional modes between the models and that the updated model accounted for the phenotypic variation caused by dominance rank and age-sex class, we elected to use the conditional modes derived from the updated model as our individual level visual tolerance estimates in this study, despite the minor decrease in ICC for the updated model.

Consistency across years

To understand whether individual visual tolerance estimates varied between years (and were therefore applicable to the 2018/19 looking analysis) we repeated the procedures outlined in (48) on a subset of 15 individuals (approximately 25% of group members) that were present across 2017, 2018, and 2019. Due to time constraints and results from the previous approach we allowed for up to 4 approaches per individual per sample day, but never sequentially. All individuals received 12 approaches by AA for the 2019 samples.

For the first part of this analysis, we combined the data collected during 2017 and 2018 with the data collected during 2019. The analysis described in (48) was repeated on this dataset. The only changes to this VOD model were that the observer identity and trial number interaction was removed (as only AA completed trials in 2019) and were replaced with individual trial number (for AA specifically) as a fixed effect and random slope over individual identity. Group trial number per day and individual trial number per day were also included as fixed effects to control for habituation and sensitization effects across a number of temporal levels. We also included 'year' as a fixed effect to explore consistency between years across all individuals. We removed the fixed effects of neighbour flee first and external factors within 5 minutes from the models used in (48) as they were previously shown not to effect FID in a significant way and we did not want to over parameterize the model. With 2017 as the reference category, the model estimates for 2018 and 2019 were 0.05 (-0.09, 0.20) and 0.09 (-0.06, 0.23) respectively. In each case estimates were close to zero with credible intervals overlapping zero, providing strong support for there being no effect of year on FID.

In addition, we ran a 2019 model using the same analytical framework as described above based only on 2019 FID data from the sample of 15 individuals. The only changes to the model was the removal of the covariate 'year'. We then extracted the individual conditional modes from the model and performed a Pearson's correlation between the 2019 conditional modes and the conditional modes from the updated model (from the main text - 2017/18 data). Results supported that tolerance estimates were consistent across years (r(13) = .77, p < .001), as such we felt confident utilising the data collected during 2017/2018 for all individuals in the updated model. Conditional modes extracted from the updated model were originally on the spectrum whereby highly tolerant animals had low/negative estimates and highly intolerant animals had high/positive estimates; therefore, tolerance was multiplied by minus 1 to reverse the scale for more logical inference in this study.

S6. Model summary results

Intercept only models

Table S2. Intercept summary results for frequency response variable. Date and individual identity fitted as crossed group-level (i.e., random) effects.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.36	0.03	-2.42	-2.3	1	1100	1740
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1	1626	2596
ID							
sd(Intercept)	0.18	0.02	0.15	0.23	1	1212	1913

Table S3. Intercept summary results for duration response variable. Date and individual identity fitted as crossed group-level (i.e., random) effects.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-95.69	17.69	-137.4	-68.99	1	2135	2031
Date							
sd(Intercept)	16.09	3.43	10.42	23.7	1	1985	2353
ID							
sd(Intercept)	24.21	4.76	16.71	35.16	1	2201	2443
Family							
sigma	34.58	3.34	29.25	42.02	1	2219	1836

Minimal models

Table S4. Frequency model summary with age-sex class and time spent engaged as population-level effects and date and individual identity fitted as crossed group-level (i.e., random) effects.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.09	0.06	-2.2	-1.98	1.01	637	1166
Time spent engaged	-0.01	0	-0.01	-0.01	1.00	4051	2939
Adolescent males	-0.46	0.1	-0.66	-0.26	1.00	1037	1996
Adult females	-0.19	0.06	-0.31	-0.07	1.00	876	1769
Adult females (Infant contact)	-0.22	0.07	-0.35	-0.09	1.00	1151	1806
Adult females (Infant OS)	-0.08	0.12	-0.31	0.15	1.00	2520	2779
Adult males	-0.42	0.08	-0.58	-0.27	1.00	943	1544
Juvenile-1 females	0.07	0.08	-0.08	0.22	1.00	1192	1822
Juvenile-1 males	-0.08	0.08	-0.24	0.07	1.00	986	1510
Juvenile-2 females	-0.06	0.06	-0.18	0.06	1.00	1505	2440
Juvenile-2 males	-0.13	0.07	-0.26	0.01	1.00	831	1726
Juvenile-3 males	-0.24	0.08	-0.41	-0.08	1.00	859	1454
Date							
sd(Intercept)	0.17	0.02	0.13	0.21	1.00	1306	2427
ID							
sd(Intercept)	0.13	0.02	0.1	0.17	1.01	1033	2280

Table S5. Duration model summary with age-sex class and time spent not engaged as population-level effects and date and individual identity fitted as crossed group-level (i.e., random) effects.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-61.28	2.08	-65.35	-57.41	1.00	1405	2274
Adolescent males	3.05	1.88	-0.59	6.74	1.00	1804	2718
Adult females	0.69	1.22	-1.7	3.15	1.00	1118	1980
Adult females (Infant contact)	1.71	1.43	-1.12	4.49	1.00	1341	2321
Adult females (Infant OS)	2.41	3.34	-4.27	8.9	1.00	3890	2896
Adult males	3.52	1.39	0.81	6.24	1.00	1247	1915
Juvenile-1 females	-2.18	1.63	-5.36	0.94	1.00	1663	2515
Juvenile-1 males	-1.87	1.54	-4.75	1.29	1.00	1604	2443
Juvenile-2 females	-0.13	1.48	-3.06	2.77	1.00	1593	2633
Juvenile-2 males	3.07	1.35	0.48	5.71	1.00	1325	2279
Juvenile-3 males	2.3	1.56	-0.78	5.37	1.00	1388	1908
Time spent not engaged	1.78	0.06	1.66	1.9	1.00	2187	2852
Date							
sd(Intercept)	2.15	0.38	1.44	2.92	1.00	1786	2250
ID							
sd(Intercept)	1.27	0.47	0.25	2.13	1.00	745	465
Family							
sigma	10.56	0.25	10.08	11.08	1.00	2132	2793

Interaction between spatial position and cohesion

Table S6. Summary results for frequency model exploring the effect of the interaction between spatial position (central/peripheral) and spatial cohesion (number of neighbours within 5 meters). The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.05	0.06	-2.17	-1.93	1.00	574	1179
Adolescent males	-0.44	0.1	-0.64	-0.25	1.00	1336	2508
Adult females	-0.19	0.06	-0.31	-0.08	1.00	583	1201
Adult females (Infant contact)	-0.19	0.07	-0.32	-0.05	1.00	818	1201
Adult females (Infant OS)	-0.08	0.12	-0.3	0.14	1.00	1979	2497
Adult males	-0.41	0.08	-0.56	-0.27	1.00	1033	2053
Juvenile-1 females	0.08	0.07	-0.07	0.23	1.00	889	1945
Juvenile-1 males	-0.04	0.08	-0.2	0.12	1.00	911	1703
Juvenile-2 females	-0.05	0.06	-0.18	0.07	1.00	1151	2068
Juvenile-2 males	-0.11	0.07	-0.25	0.02	1.00	831	1489
Juvenile-3 males	-0.22	0.08	-0.38	-0.05	1.00	880	1408
Spatial position (Peripheral)	0.08	0.03	0.02	0.14	1.00	2724	2755
Number of neighbours (5m)	-0.04	0.01	-0.05	-0.02	1.00	3344	3139
Time spent engaged	-0.01	0	-0.01	-0.01	1.00	4248	3574
Peripheral : Number of neighbours	-0.02	0.01	-0.04	0.01	1.00	2650	2739
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1.00	1410	2233
ID							
sd(Intercept)	0.13	0.02	0.1	0.16	1.00	1661	2309

Table S7. Summary results for duration model exploring the effect of the interaction between spatial position (central/peripheral) and spatial cohesion (number of neighbours within 5 meters). The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-61.22	2.16	-65.57	-57.21	1.00	1408	1396
Adolescent males	3.12	1.83	-0.37	6.67	1.00	1964	2507
Adult females	0.68	1.19	-1.71	2.99	1.01	1038	1648
Adult females (Infant contact)	1.81	1.45	-1.11	4.68	1.00	1286	2016
Adult females (Infant OS)	2.41	3.38	-4.54	8.77	1.00	3621	2719
Adult males	3.6	1.35	0.85	6.28	1.00	1162	1812
Juvenile-1 females	-2.1	1.6	-5.33	1.17	1.00	1575	1992
Juvenile-1 males	-1.79	1.52	-4.67	1.19	1.00	1501	2109
Juvenile-2 females	-0.09	1.47	-3.04	2.78	1.00	1574	2333
Juvenile-2 males	3.1	1.35	0.33	5.67	1.00	1362	1943
Juvenile-3 males	2.35	1.57	-0.72	5.42	1.00	1449	2142
Spatial position (Peripheral)	0.14	0.76	-1.34	1.61	1.00	3634	3579
Number of neighbours (5m)	-0.1	0.16	-0.42	0.23	1.00	3926	3062
Time spent engaged	1.78	0.06	1.67	1.91	1.00	1949	2220
Peripheral : Number of neighbours	-0.15	0.31	-0.76	0.43	1.00	3618	3007
Date							
sd(Intercept)	2.11	0.38	1.4	2.89	1.00	1318	2281
ID							
sd(Intercept)	1.25	0.5	0.14	2.16	1.00	735	490
Family							
sigma	10.58	0.26	10.09	11.09	1.00	1905	2563

Table S8. Summary results for frequency model exploring the effect of foraging success and predominant foraging item on looking behaviours. The remainder of the population-level and group-level factors are the same as the minimal model. *Acacia/Senegalia ataxacantha* seeds pods and adolescent females embedded within the intercept.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.01	0.07	-2.15	-1.86	1.00	1189	2005
Amount Eaten	0.02	0	0.01	0.02	1.00	6562	3501
Acacia/Vachellia karoo seed pods	-0.05	0.06	-0.18	0.07	1.00	1312	2047
Acacia/Vachellia sieberiana seed pods	0.73	0.08	0.57	0.89	1.00	1585	2588
Grass corm	0.23	0.11	0.02	0.45	1.00	2222	2840
Dichrostachys cinerea seed pods	0.35	0.07	0.22	0.48	1.00	1334	2506
Fruit (Small)	0.01	0.07	-0.14	0.14	1.00	1335	2268
Fruit (Large)	0.3	0.08	0.14	0.47	1.00	1708	2959
Grass blades	0.2	0.06	0.09	0.32	1.00	1107	2465
Grass seeds	0.15	0.08	0	0.3	1.00	1722	2455
Inverterbates	0.03	0.09	-0.15	0.2	1.00	1904	2771
Leaves	0.13	0.1	-0.06	0.31	1.00	2521	2581
No food eaten	-0.57	0.06	-0.68	-0.46	1.00	955	1894
Other	0.14	0.11	-0.07	0.35	1.00	3160	2976
Roots	0.18	0.06	0.07	0.29	1.00	936	1804
Succulent leaves	0.41	0.11	0.2	0.62	1.00	2293	2894
Unknown	0.07	0.07	-0.07	0.21	1.00	1358	1898
Seeds in leaf litter	0.18	0.07	0.04	0.32	1.00	1544	2167
Ziziphus mucronata fruit	0.24	0.1	0.04	0.43	1.00	2413	2719
Ziziphus mucronata seed	0.26	0.09	0.09	0.44	1.00	2198	2599
Adolescent males	-0.29	0.1	-0.47	-0.1	1.00	2322	2915
Adult females	-0.12	0.05	-0.22	-0.01	1.00	1479	2672
Adult females (Infant contact)	-0.1	0.06	-0.22	0.02	1.00	1985	2876
Adult females (Infant OS)	-0.12	0.12	-0.36	0.1	1.00	4130	3059
Adult males	-0.26	0.07	-0.4	-0.12	1.00	1562	2414
Juvenile-1 females	0.06	0.07	-0.07	0.2	1.00	1899	2346
Juvenile-1 males	-0.08	0.07	-0.22	0.06	1.00	1862	2546
Juvenile-2 females	-0.05	0.06	-0.17	0.06	1.00	2148	2553
Juvenile-2 males	-0.09	0.06	-0.21	0.03	1.00	1779	2403
Juvenile-3 males	-0.21	0.07	-0.35	-0.06	1.00	1950	2557
Time spent engaged	-0.02	0	-0.02	-0.02	1.00	5026	3978

Table S9. Summary results for duration model exploring the effect of foraging success and predominant foraging item on looking behaviours. The remainder of the population-level and group-level factors are the same as the minimal model. *Acacia/Senegalia ataxacantha* seeds pods and adolescent females embedded within the intercept.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-49.79	2.17	-54.05	-45.58	1.01	1207	1906
Amount Eaten	-0.45	0.07	-0.59	-0.32	1.00	4402	3015
Acacia/Vachellia karoo seed pods	-1.84	2.11	-5.93	2.48	1.00	1456	2203
Acacia/Vachellia sieberiana seed pods	-4.87	2.75	-10.37	0.33	1.00	1653	2284
Grass corm	-8.32	3.41	-14.92	-1.77	1.00	2825	2761
Dichrostachys cinerea seed pods	-10.03	2.02	-14.06	-6.12	1.00	1222	2386
Fruit (Small)	1.16	2.03	-2.88	5.09	1.00	1117	2081
Fruit (Large)	-0.22	2.18	-4.43	4.08	1.00	1524	2452
Grass blades	8.31	1.71	4.99	11.75	1.00	875	1767
Grass seeds	4.67	2.13	0.44	8.97	1.00	1253	1945
Inverterbates	0.34	2.34	-4.23	4.87	1.00	1518	2399
Leaves	7.99	2.74	2.61	13.29	1.00	1819	2167
No food eaten	0.75	1.51	-2.15	3.7	1.00	809	1486
Other	-2.51	2.8	-8.26	2.81	1.00	1819	2381
Roots	-8.66	1.63	-11.87	-5.47	1.00	883	1544
Succulent leaves	-4.7	3.21	-11.06	1.53	1.00	2028	2698
Unknown	-1.55	1.8	-5.05	2	1.00	1043	1977
Seeds in leaf litter	-1.13	2.04	-5.25	2.86	1.00	1125	1890
Ziziphus mucronata fruit	-4.29	2.56	-9.31	0.69	1.00	1722	2386
Ziziphus mucronata seed	-4.26	2.32	-8.93	0.15	1.00	1493	2624
Adolescent males	1.3	1.6	-1.89	4.42	1.00	1940	2494
Adult females	-0.12	1.07	-2.27	1.95	1.00	1238	1670
Adult females (Infant contact)	0.15	1.26	-2.33	2.65	1.00	1553	2343
Adult females (Infant OS)	2.37	2.86	-3.36	7.86	1.00	3987	3215
Adult males	1.61	1.2	-0.74	3.95	1.00	1212	2172
Juvenile-1 females	-1.88	1.4	-4.59	0.87	1.00	1602	2518
Juvenile-1 males	-1.93	1.36	-4.67	0.71	1.00	1456	2232
Juvenile-2 females	0.02	1.3	-2.58	2.55	1.00	1851	2452
Juvenile-2 males	2.12	1.18	-0.24	4.39	1.00	1228	1959
Juvenile-3 males	1.77	1.39	-1.02	4.36	1.00	1510	2480
Time spent engaged	1.47	0.05	1.38	1.57	1.00	2486	2737
Date							
sd(Intercept)	1.37	0.35	0.61	2.02	1.00	1157	1250
ID							
sd(Intercept)	1.19	0.42	0.23	1.95	1.00	747	527
Family							
sigma	9.29	0.21	8.91	9.73	1.00	2370	2788

Reactionary models

Table S10. Model summary results for all reactionary models with the frequency response variable, displaying parameter estimates and credible intervals. In all cases the bulk effective sample size was greater than 100 times the number of chains (i.e., Bulk ESS > 400) indicating efficient sampling of the mean of the distributions. The Gelman-Rubin convergence diagnostic was less than 1.01 in all cases suggesting accurate estimates of the posterior distributions. Bold text highlights where credible intervals did not overlap or include zero. None of these models shared considerable weight when stacked. IE refers to inter-species (or heterospecific) encounters. WE refers to within-species encounters (i.e., foreign males or other groups).

	Aggression	Mating	Female calls	Male calls	Passive IE	Active IE	Alarm	Dog encounter	WE
Intercept	**-2.24 (-2.43, -2.04)**	**-2.16 (-2.31, -2.01)**	**-1.88 (-2.02, -1.73)**	**-2.36 (-2.57, -2.15)**	**-2.09 (-2.27, -1.91)**	**-2.38 (-2.75, -2.02)**	**-1.96 (-2.2, -1.72)**	**-1.75 (-2, -1.5)**	**-2.35 (-2.59, -2.12)**
No event	**-0.27 (-0.39, -0.15)**	**0.06 (-0.06, 0.18)**	**-0.26 (-0.37, -0.16)**	-0.08 (-0.22, 0.05)	-0.05 (-0.2, 0.11)	0.08 (-0.22, 0.38)	-0.13 (-0.32, 0.06)	**-0.31 (-0.51, -0.11)**	0.11 (-0.05, 0.28)
Event ongoing	0 (-0.11, 0.12)	0.08 (-0.18, 0.33)	**-0.2 (-0.35, -0.04)**	-0.12 (-0.3, 0.06)	0.01 (-0.16, 0.18)	0.22 (-0.2, 0.63)	-0.17 (-0.5, 0.15)	-0.13 (-0.46, 0.19)	-0.07 (-0.25, 0.1)
5 - 10 mins post event	-0.08 (-0.16, 0.01)	-0.06 (-0.22, 0.09)	-0.15 (-0.3, 0)	0.08 (-0.04, 0.21)	0.21 (0.03, 0.4)	0.18 (-0.21, 0.57)	-0.01 (-0.26, 0.24)	-0.06 (-0.35, 0.23)	0.15 (-0.06, 0.37)
10 - 15 mins post event	**-0.14 (-0.23, -0.05)**	0.06 (-0.1, 0.21)	-0.08 (-0.23, 0.06)	0 (-0.13, 0.14)	0.21 (0, 0.42)	-0.46 (-1, 0.07)	-0.1 (-0.37, 0.18)	-0.19 (-0.51, 0.14)	0.05 (-0.17, 0.26)
15 + mins post event	**-0.08 (-0.15, -0.02)**	0.09 (-0.01, 0.2)	**-0.23 (-0.32, -0.13)**	0.05 (-0.05, 0.15)	0.03 (-0.12, 0.18)	0.02 (-0.27, 0.33)	-0.07 (-0.25, 0.13)	**-0.3 (-0.5, -0.1)**	0.14 (-0.01, 0.3)
Rank	0 (0, 0.01)			0 (0, 0.01)		0 (0, 0.01)			0 (0, 0.01)
Visibility	0 (0, 0)			0 (0, 0)		0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Tolerance									
Spatial position (Peripheral)							**0.05 (0.01, 0.09)**	0.05 (0, 0.09)	0.05 (0, 0.09)
Number of neighbours (5m)							**-0.04 (-0.05, -0.03)**	**-0.04 (-0.06, -0.03)**	**-0.04 (-0.05, -0.03)**
Time spent engaged	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**	**-0.01 (-0.01, -0.01)**
Adolescent males	**-0.29 (-0.51, -0.08)**	**-0.47 (-0.66, -0.26)**	**-0.45 (-0.64, -0.25)**	**-0.29 (-0.51, -0.07)**	**-0.46 (-0.66, -0.26)**	**-0.3 (-0.53, -0.08)**	**-0.44 (-0.64, -0.25)**	**-0.43 (-0.63, -0.23)**	**-0.32 (-0.54, -0.09)**
Adult females	**-0.15 (-0.26, -0.03)**	**-0.19 (-0.3, -0.07)**	**-0.19 (-0.3, -0.07)**	**-0.16 (-0.27, -0.04)**	**-0.19 (-0.31, -0.08)**	**-0.16 (-0.28, -0.05)**	**-0.19 (-0.3, -0.08)**	**-0.19 (-0.31, -0.08)**	**-0.17 (-0.28, -0.06)**
Adult females (Infant contact)	**-0.18 (-0.31, -0.05)**	**-0.22 (-0.35, -0.08)**	**-0.21 (-0.34, -0.08)**	**-0.19 (-0.32, -0.06)**	**-0.22 (-0.34, -0.09)**	**-0.19 (-0.32, -0.07)**	**-0.18 (-0.31, -0.05)**	**-0.19 (-0.32, -0.06)**	**-0.17 (-0.29, -0.04)**
Adult females (Infant OS)	**-0.05 (-0.29, 0.18)**	-0.08 (-0.32, 0.15)	-0.07 (-0.29, 0.15)	-0.05 (-0.28, 0.19)	-0.08 (-0.32, 0.16)	-0.05 (-0.29, 0.18)	-0.07 (-0.31, 0.15)	-0.07 (-0.31, 0.15)	-0.06 (-0.3, 0.16)
Adult males	**-0.24 (-0.43, -0.06)**	**-0.43 (-0.58, -0.28)**	**-0.42 (-0.57, -0.28)**	**-0.25 (-0.43, -0.06)**	**-0.43 (-0.58, -0.28)**	**-0.25 (-0.44, -0.07)**	**-0.41 (-0.56, -0.26)**	**-0.41 (-0.56, -0.26)**	**-0.26 (-0.44, -0.08)**
Juvenile-1 females	**0.07 (-0.07, 0.21)**	0.07 (-0.08, 0.21)	0.07 (-0.08, 0.22)	0.06 (-0.08, 0.21)	0.06 (-0.08, 0.21)	0.06 (-0.09, 0.2)	0.08 (-0.06, 0.23)	0.08 (-0.07, 0.22)	0.08 (-0.07, 0.22)
Juvenile-1 males	**-0.01 (-0.17, 0.14)**	-0.08 (-0.24, 0.07)	-0.07 (-0.23, 0.08)	-0.02 (-0.17, 0.13)	-0.08 (-0.24, 0.06)	-0.02 (-0.18, 0.13)	-0.03 (-0.19, 0.12)	-0.04 (-0.19, 0.12)	0 (-0.14, 0.16)
Juvenile-2 females	**-0.06 (-0.18, 0.06)**	-0.06 (-0.19, 0.06)	-0.06 (-0.18, 0.07)	-0.06 (-0.19, 0.06)	-0.07 (-0.19, 0.05)	-0.07 (-0.19, 0.06)	-0.05 (-0.17, 0.08)	-0.05 (-0.17, 0.07)	-0.06 (-0.18, 0.06)
Juvenile-2 males	**-0.06 (-0.2, 0.07)**	-0.13 (-0.26, 0.01)	-0.12 (-0.26, 0.02)	-0.07 (-0.21, 0.07)	-0.13 (-0.27, 0)	-0.08 (-0.22, 0.06)	-0.11 (-0.24, 0.03)	-0.11 (-0.25, 0.02)	-0.06 (-0.2, 0.08)
Juvenile-3 males	**-0.11 (-0.28, 0.07)**	**-0.25 (-0.41, -0.08)**	**-0.23 (-0.4, -0.06)**	-0.11 (-0.28, 0.08)	**-0.25 (-0.41, -0.08)**	-0.12 (-0.3, 0.06)	**-0.22 (-0.38, -0.07)**	**-0.21 (-0.38, -0.05)**	-0.11 (-0.28, 0.07)
Date									
sd(Intercept)	0.16 (0.13, 0.2)	0.17 (0.13, 0.21)	0.16 (0.13, 0.2)	0.16 (0.13, 0.2)	0.17 (0.13, 0.2)	0.17 (0.14, 0.21)	0.15 (0.12, 0.19)	0.16 (0.13, 0.2)	0.16 (0.13, 0.2)
ID									
sd(Intercept)	0.12 (0.1, 0.16)	0.13 (0.1, 0.17)	0.13 (0.1, 0.17)	0.13 (0.1, 0.17)	0.13 (0.1, 0.17)	0.12 (0.09, 0.16)	0.13 (0.1, 0.16)	0.13 (0.1, 0.17)	0.12 (0.09, 0.16)

Table S11. Model summary results for all reactionary models with the duration response variable, displaying parameter estimates and credible intervals. In all cases the bulk effective sample size was greater than 100 times the number of chains (i.e., Bulk ESS > 400) indicating efficient sampling of the mean of the distributions. The Gelman-Rubin convergence diagnostic was less than 1.01 in all cases suggesting accurate estimates of the posterior distributions. Bold text highlights where credible intervals did not overlap or include zero. Only time since wahoo and within-species encounter models had considerable weight when stacked. IE refers to inter-species (or heterospecific) encounters. WE refers to within-species encounters (i.e., foreign males or other groups).

	Aggression	Mating	Female calls	Male calls	Passive IE	Active IE	Alarm	DE	WE
Intercept	**-70.31 (-76.41, -64.97)**	**-59.1 (-64.14, -54.43)**	**-61.72 (-67, -56.89)**	**-67.06 (-73.17, -61.69)**	**-64.28 (-70.24, -58.59)**	**-81.84 (-91.64, -72.22)**	**-68.17 (-75.3, -61.68)**	**-72.47 (-80.16, -65.29)**	**-68.46 (-75.14, -62.37)**
No event	-0.32 (-2.59, 2.01)	-2.66 (-6.24, 0.93)	1.81 (-2.45, 5.88)	-2.45 (-5.75, 0.9)	1.7 (-4.1, 7.57)	**19.98 (9.21, 31.42)**	1.88 (-4.68, 8.38)	-0.49 (-9.06, 8)	-2.65 (-8.13, 2.69)
Event ongoing	0.32 (-1.27, 1.9)	-2.4 (-4.97, 0.12)	0.09 (-2.68, 2.93)	**-2.94 (-5.21, -0.61)**	2.67 (-1.33, 6.74)	**12.62 (4.94, 20.81)**	-2.23 (-6.74, 2.51)	0.98 (-4.36, 6.67)	-0.58 (-4.23, 3.14)
5 - 10 mins post event	1.01 (-1.18, 3.16)	-1.24 (-4.78, 2.34)	2.44 (-1.82, 6.57)	-1.56 (-4.67, 1.6)	1.36 (-4.07, 6.77)	**10.74 (1.02, 20.77)**	-1.6 (-7.81, 4.91)	-2.47 (-10.96, 5.65)	-3.8 (-8.93, 1.39)
10 - 15 mins post event	**6.94 (4.02, 9.68)**	-1.03 (-7.32, 5.15)	1.58 (-2.59, 5.66)	**6.47 (2.49, 10.4)**	0.17 (-4.15, 4.65)	**13.59 (2.19, 25.06)**	**7.94 (0.6, 15.43)**	4.3 (-3.99, 12.55)	**5.32 (1.44, 9.38)**
15 + mins post event	1.99 (-0.7, 4.56)	-2.02 (-4.69, 0.66)	0.91 (-2.12, 3.91)	-0.08 (-3.13, 2.93)	3.86 (-0.12, 8.03)	**11.18 (3.7, 19.42)**	-1.75 (-6.21, 2.96)	1.98 (-3.3, 7.57)	0.43 (-3.24, 4.2)
Rank	-0.01 (-0.05, 0.02)			-0.01 (-0.05, 0.03)		-0.01 (-0.04, 0.03)			-0.01 (-0.05, 0.03)
Visibility	**0.14 (0.11, 0.18)**			**0.14 (0.11, 0.17)**		**0.14 (0.11, 0.17)**	**0.14 (0.1, 0.17)**	**0.14 (0.11, 0.18)**	**0.13 (0.1, 0.16)**
Tolerance									
Spatial position (Peripheral)							-0.16 (-1.19, 0.84)	-0.15 (-1.2, 0.9)	-0.29 (-1.33, 0.72)
Number of neighbours (5m)							-0.1 (-0.38, 0.17)	-0.1 (-0.36, 0.17)	-0.17 (-0.45, 0.1)
Time spent not engaged	**1.73 (1.62, 1.85)**	**1.78 (1.67, 1.91)**	**1.78 (1.66, 1.91)**	**1.72 (1.61, 1.84)**	**1.78 (1.66, 1.91)**	**1.74 (1.63, 1.86)**	**1.74 (1.63, 1.86)**	**1.75 (1.63, 1.87)**	**1.72 (1.61, 1.84)**
Adolescent males	1.82 (-2.21, 5.79)	2.92 (-0.67, 6.64)	3.02 (-0.75, 6.78)	1.92 (-2.08, 5.88)	3.1 (-0.52, 6.8)	2.31 (-1.38, 6.32)	2.55 (-0.94, 6.21)	2.53 (-1.09, 6.11)	2.18 (-1.71, 6.14)
Adult females	0.25 (-2.08, 2.59)	0.62 (-1.72, 3.04)	0.65 (-1.82, 3.09)	0.41 (-1.97, 2.88)	0.79 (-1.61, 3.27)	0.57 (-1.74, 2.88)	0.55 (-1.78, 2.93)	0.47 (-1.86, 2.79)	0.4 (-1.94, 2.73)
Adult females (Infant contact)	1.35 (-1.46, 4.08)	1.64 (-1.21, 4.57)	1.62 (-1.35, 4.52)	1.43 (-1.3, 4.25)	1.85 (-0.93, 4.66)	1.68 (-1.09, 4.44)	1.68 (-1.13, 4.39)	1.6 (-1.05, 4.3)	1.47 (-1.17, 4.24)
Adult females (Infant OS)	1.69 (-5.04, 7.95)	2.41 (-4.05, 8.91)	2.33 (-4.31, 9.06)	1.66 (-4.34, 7.93)	2.81 (-3.78, 9.18)	2.24 (-4.31, 8.2)	2.29 (-3.88, 8.33)	2.25 (-4.07, 8.62)	2.22 (-4.2, 8.53)
Adult males	2.11 (-1.09, 5.33)	**3.43 (0.75, 6.19)**	**3.5 (0.81, 6.17)**	2.2 (-1.1, 5.4)	**3.56 (0.8, 6.32)**	2.51 (-0.59, 5.61)	**2.87 (0.28, 5.41)**	**2.79 (0.11, 5.42)**	2.2 (-0.94, 5.4)
Juvenile-1 females	-2.28 (-5.35, 0.77)	-2.21 (-5.42, 0.97)	-2.24 (-5.47, 0.92)	-2.06 (-5.27, 0.99)	-2.11 (-5.4, 1.02)	-2.17 (-5.25, 0.88)	-2.19 (-5.39, 0.87)	-2.17 (-5.4, 0.91)	-2.04 (-5.15, 0.94)
Juvenile-1 males	-2.19 (-5.21, 0.79)	-1.95 (-4.95, 1.04)	-1.96 (-5.02, 1.16)	-1.89 (-4.93, 1.15)	-1.64 (-4.67, 1.42)	-2 (-4.91, 0.94)	-1.77 (-4.77, 1.2)	-1.78 (-4.64, 1.07)	-1.7 (-4.71, 1.27)
Juvenile-2 females	-0.57 (-3.26, 2.27)	-0.18 (-2.96, 2.78)	-0.14 (-3.12, 2.78)	-0.17 (-3.09, 2.78)	-0.05 (-2.84, 2.84)	-0.28 (-3.15, 2.57)	-0.41 (-3.21, 2.55)	-0.46 (-3.35, 2.35)	-0.31 (-3.14, 2.46)
Juvenile-2 males	2.13 (-0.57, 4.75)	**2.99 (0.39, 5.7)**	**3.03 (0.28, 5.75)**	2.33 (-0.37, 5.01)	**3.18 (0.48, 5.83)**	**2.65 (0.05, 5.32)**	2.55 (-0.05, 5.14)	2.54 (-0.03, 5.1)	2.15 (-0.4, 4.78)
Juvenile-3 males	1.24 (-2.08, 4.7)	2.18 (-0.85, 5.31)	2.28 (-0.95, 5.41)	1.33 (-2.19, 4.69)	2.34 (-0.8, 5.4)	1.55 (-1.65, 4.69)	1.7 (-1.38, 4.82)	1.72 (-1.27, 4.65)	1.14 (-2.08, 4.37)
Date									
sd(Intercept)	2.07 (1.35, 2.85)	2.14 (1.4, 2.94)	2.17 (1.41, 2.97)	2 (1.28, 2.75)	2.16 (1.45, 2.91)	2.11 (1.39, 2.91)	2.04 (1.31, 2.82)	2.02 (1.3, 2.75)	1.95 (1.23, 2.7)
ID									
sd(Intercept)	1.23 (0.24, 2.11)	1.28 (0.33, 2.13)	1.28 (0.15, 2.19)	1.21 (0.2, 2.08)	1.28 (0.22, 2.2)	1.16 (0.13, 2.05)	1.21 (0.17, 2.08)	1.13 (0.15, 2.02)	1.09 (0.1, 1.98)
Family									
sigma	10.34 (9.88, 10.87)	10.57 (10.09, 11.11)	10.56 (10.08, 11.08)	10.3 (9.83, 10.79)	10.56 (10.07, 11.08)	10.36 (9.89, 10.87)	10.36 (9.89, 10.88)	10.42 (9.93, 10.92)	10.31 (9.85, 10.8)

Table S12. Summary results for model exploring the relationship between the frequency of looking bouts and the number of social threats within 5 meters. Also included are dominance rank of the focal animal, number of neighbours within 5 meters, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.14	0.1	-2.32	-1.95	1.00	1418	2279
Count of social threats in 5 meters	0.08	0.01	0.05	0.1	1.00	3177	2930
Time spent engaged	-0.01	0	-0.01	-0.01	1.00	4029	3149
Dominance rank	0	0	0	0	1.00	1804	2753
Number of neighbours within 5 meters	-0.08	0.01	-0.09	-0.06	1.00	3179	3211
Visibility	0	0	0	0	1.00	4248	2811
Adolescent males	-0.32	0.11	-0.53	-0.1	1.00	1542	2139
Adult females	-0.17	0.06	-0.28	-0.05	1.00	1175	1980
Adult females (Infant contact)	-0.17	0.07	-0.3	-0.04	1.00	1322	2318
Adult females (Infant OS)	-0.06	0.12	-0.29	0.18	1.00	2555	2912
Adult males	-0.26	0.09	-0.44	-0.07	1.00	1188	1815
Juvenile-1 females	0.08	0.07	-0.07	0.22	1.00	1462	2263
Juvenile-1 males	0	0.08	-0.15	0.16	1.00	1123	2006
Juvenile-2 females	-0.06	0.06	-0.18	0.06	1.00	1726	2376
Juvenile-2 males	-0.08	0.07	-0.21	0.06	1.00	1085	2128
Juvenile-3 males	-0.13	0.09	-0.31	0.05	1.00	1270	2066
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1.00	1496	2178
ID							
sd(Intercept)	0.12	0.02	0.09	0.16	1.00	1735	2752

Table S13. Summary results for model exploring the relationship between the total duration of looking bouts and the number of social threats within 5 meters. Also included are dominance rank of the focal animal, number of neighbours within 5 meters, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-68.34	2.72	-73.63	-63.24	1.00	1609	2364
Count of social threats in 5 meters	1.27	0.32	0.63	1.91	1.00	3084	3308
Number of neighbours within 5 meters	-0.55	0.17	-0.89	-0.22	1.00	3346	3086
Dominance rank	-0.04	0.02	-0.08	0	1.00	2231	2412
Visibility	0.14	0.02	0.11	0.17	1.00	4878	3252
Time spent not engaged	1.73	0.06	1.62	1.85	1.00	2063	2581
Adolescent males	1.66	2.04	-2.33	5.64	1.00	1423	2074
Adult females	0.14	1.22	-2.31	2.48	1.00	1139	2082
Adult females (Infant contact)	1.17	1.43	-1.74	3.96	1.00	1421	2318
Adult females (Infant OS)	2.35	3.21	-3.99	8.64	1.00	3487	2875
Adult males	1.95	1.69	-1.36	5.28	1.00	1099	1695
Juvenile-1 females	-2.33	1.59	-5.49	0.74	1.00	1791	2489
Juvenile-1 males	-2.22	1.57	-5.28	0.9	1.00	1547	2470
Juvenile-2 females	-0.58	1.44	-3.44	2.19	1.00	1791	3070
Juvenile-2 males	1.98	1.39	-0.76	4.67	1.00	1291	2272
Juvenile-3 males	0.82	1.72	-2.6	4.07	1.00	1154	2096
Date							
sd(Intercept)	2.01	0.38	1.3	2.8	1.00	1458	1998
ID							
sd(Intercept)	1.3	0.45	0.34	2.12	1.00	999	954
Family							
sigma	10.33	0.25	9.87	10.84	1.00	1838	2639

Table S14. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between probability of occurrence of leopards and several other reported risk factors, including time spent engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-1.97	0.15	-2.26	-1.69	1.00	1902	2485
Leopard risk	-0.38	0.17	-0.7	-0.06	1.00	2355	2794
Number of neighbours (5m)	-0.17	0.03	-0.23	-0.11	1.00	2741	2860
Spatial position (Peripheral)	-0.23	0.11	-0.45	-0.01	1.00	2789	2859
Time spent engaged	-0.01	0	-0.02	0	1.00	3778	2684
Visibility	0	0	0	0	1.00	4524	3213
Rank	0	0	0	0.01	1.00	2154	2467
Adolescent males	-0.31	0.11	-0.53	-0.1	1.01	1344	2025
Adult females	-0.17	0.06	-0.28	-0.05	1.00	1181	2178
Adult females (Infant contact)	-0.16	0.07	-0.29	-0.04	1.00	1492	2526
Adult females (Infant OS)	-0.06	0.12	-0.3	0.17	1.00	2974	2801
Adult males	-0.27	0.09	-0.44	-0.08	1.00	1277	2005
Juvenile-1 females	0.08	0.07	-0.06	0.22	1.00	1693	2311
Juvenile-1 males	0.01	0.08	-0.14	0.16	1.00	1262	2255
Juvenile-2 females	-0.06	0.06	-0.18	0.06	1.00	1901	2938
Juvenile-2 males	-0.07	0.07	-0.21	0.07	1.00	1080	1675
Juvenile-3 males	-0.11	0.09	-0.28	0.07	1.00	1226	1869
Leopard risk : Number of neighbours	0.19	0.05	0.1	0.29	1.00	2734	2747
Leopard risk : Spatial position (Peripheral)	0.41	0.17	0.08	0.74	1.00	2800	2739
Leopard risk : Time spent engaged	0	0.01	-0.02	0.01	1.00	3763	2741
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1.00	1327	1953
ID							
sd(Intercept)	0.12	0.02	0.09	0.16	1.00	1748	2503

Table S15. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between probability of occurrence of leopards and several other reported risk factors, including time spent not engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-60.58	5.83	-71.91	-49.17	1.00	3458	3325
Leopard risk	-13.99	7.73	-29.64	0.99	1.00	3527	2937
Number of neighbours (5m)	-1.29	0.73	-2.69	0.14	1.00	5192	3446
Spatial position (Peripheral)	1.96	2.68	-3.35	7.19	1.00	5272	3199
Time spent not engaged	1.33	0.19	0.96	1.7	1.00	3783	3054
Visibility	0.14	0.02	0.1	0.17	1.00	8330	3240
Rank	-0.01	0.02	-0.05	0.03	1.00	4045	3121
Adolescent males	1.98	2.05	-2.03	5.94	1.00	2363	2830
Adult females	0.4	1.21	-1.93	2.79	1.00	1707	2416
Adult females (Infant contact)	1.47	1.43	-1.27	4.24	1.00	1950	3102
Adult females (Infant OS)	2.25	3.29	-4.35	8.62	1.00	5582	3011
Adult males	2.42	1.67	-0.95	5.58	1.00	1843	2509
Juvenile-1 females	-2.02	1.55	-5.09	0.99	1.00	2351	2828
Juvenile-1 males	-1.85	1.55	-4.85	1.13	1.00	2307	2915
Juvenile-2 females	-0.29	1.45	-3.08	2.55	1.00	2432	3181
Juvenile-2 males	2.44	1.38	-0.21	5.18	1.00	1875	2519
Juvenile-3 males	1.46	1.74	-2.11	4.75	1.00	1869	2809
Leopard risk : Number of neighbours	1.83	1.11	-0.3	3.99	1.00	4950	3317
Leopard risk : Spatial position (Peripheral)	-3.02	4	-10.8	4.74	1.00	5042	3022
Leopard risk : Time spent not engaged	0.62	0.27	0.1	1.16	1.00	3748	2904
Date							
sd(Intercept)	2.04	0.37	1.36	2.84	1.00	1680	2559
ID							
sd(Intercept)	1.17	0.46	0.18	2.04	1.00	1174	1220
Family							
sigma	10.38	0.25	9.9	10.9	1.00	4636	2590

Table S16. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between habitat type and several other reported risk factors, including time spent engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.25	0.13	-2.52	-2	1.00	928	1611
Camp	-0.02	0.12	-0.27	0.22	1.00	893	1564
Farm	0.04	0.16	-0.26	0.35	1.00	978	1733
Forest	-0.41	0.13	-0.69	-0.16	1.00	901	1903
Grassland	0.13	0.1	-0.08	0.33	1.00	623	1232
Road	-0.03	0.12	-0.28	0.21	1.00	722	1640
Rock	-0.33	0.15	-0.61	-0.03	1.00	945	2037
Woodland	0.07	0.11	-0.14	0.28	1.00	708	1376
Spatial position (Peripheral)	0.12	0.1	-0.08	0.31	1.00	789	1257
Number of neighbours (5m)	-0.01	0.03	-0.07	0.06	1.00	734	1222
Time spent engaged	-0.01	0	-0.02	-0.01	1.00	1391	2139
Rank	0	0	0	0.01	1.00	1862	2406
Visibility	0	0	0	0	1.00	4307	3030
Adolescent males	-0.3	0.11	-0.51	-0.07	1.01	1519	2739
Adult females	-0.15	0.06	-0.26	-0.03	1.01	1029	1501
Adult females (Infant contact)	-0.16	0.07	-0.29	-0.03	1.01	1268	1903
Adult females (Infant OS)	-0.07	0.12	-0.32	0.17	1.00	2553	2396
Adult males	-0.25	0.09	-0.43	-0.07	1.01	1121	2241
Juvenile-1 females	0.08	0.07	-0.06	0.22	1.00	1594	2116
Juvenile-1 males	0.01	0.08	-0.14	0.17	1.00	1007	1759
Juvenile-2 females	-0.03	0.06	-0.16	0.08	1.00	1834	2244
Juvenile-2 males	-0.07	0.07	-0.2	0.07	1.01	1136	1562
Juvenile-3 males	-0.12	0.09	-0.29	0.06	1.01	1009	2058
Camp : Peripheral	-0.04	0.12	-0.27	0.18	1.00	1048	1633
Farm : Peripheral	0.11	0.14	-0.19	0.39	1.00	1094	1928
Forest : Peripheral	-0.17	0.14	-0.45	0.12	1.00	1283	2029
Grassland : Peripheral	-0.09	0.1	-0.29	0.11	1.00	828	1452
Road : Peripheral	-0.13	0.12	-0.37	0.11	1.00	1025	1541
Rock : Peripheral	-0.34	0.15	-0.62	-0.05	1.00	1298	1879
Woodland : Peripheral	-0.08	0.11	-0.28	0.13	1.00	914	1265
Camp : Number of neighbours	-0.01	0.04	-0.09	0.07	1.00	890	1707
Farm : Number of neighbours	-0.01	0.05	-0.11	0.08	1.00	1152	1973
Forest : Number of neighbours	-0.02	0.04	-0.1	0.07	1.00	1044	1887
Grassland : Number of neighbours	-0.05	0.03	-0.11	0.02	1.00	747	1496
Road : Number of neighbours	-0.02	0.04	-0.1	0.06	1.00	838	1805
Rock : Number of neighbours	-0.03	0.04	-0.11	0.05	1.00	938	1914
Woodland : Number of neighbours	-0.02	0.04	-0.09	0.05	1.00	793	1530
Camp : Time engaged	0.01	0	0	0.02	1.00	1756	2659
Farm : Time engaged	0.01	0.01	0	0.02	1.00	2143	3135
Forest : Time engaged	0.01	0.01	0	0.02	1.00	1868	2585
Grassland : Time engaged	0	0	-0.01	0.01	1.00	1497	2248

Road : Time engaged	0.01	0.01	0	0.02	1.00	1716	2392
Rock : Time engaged	0	0.01	-0.01	0.01	1.00	1988	2348
Woodland : Time engaged	0	0	-0.01	0.01	1.00	1475	1975
Date							
sd(Intercept)	0.16	0.02	0.12	0.19	1.00	1284	2328
ID							
sd(Intercept)	0.12	0.02	0.09	0.15	1.00	1485	2316

Table S17. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between habitat type and several other reported risk factors, including time spent not engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-63.47	5.06	-73.63	-53.8	1.00	556	1355
Camp	-4.8	5.53	-15.42	6.31	1.00	596	1085
Farm	0.72	6.36	-11.77	13.02	1.00	715	1527
Forest	-12.62	6.31	-25.4	-0.34	1.00	706	1442
Grassland	-3.68	4.68	-12.63	5.57	1.01	474	930
Road	0.88	5.37	-9.69	11.23	1.00	596	1215
Rock	-6.09	6.16	-18.11	6.1	1.00	718	1369
Woodland	-9.53	4.77	-18.74	-0.12	1.00	498	1032
Spatial position (Peripheral)	-1.1	2.7	-6.62	4.16	1.00	451	1011
Number of neighbours (5m)	-1.34	0.9	-3.12	0.4	1.00	581	1267
Time spent not engaged	1.63	0.16	1.33	1.94	1.01	607	1072
Rank	-0.01	0.02	-0.05	0.03	1.00	2368	2382
Visibility	0.13	0.02	0.09	0.16	1.00	6475	3013
Adolescent males	2.25	2.04	-1.7	6.34	1.00	1291	2253
Adult females	0.41	1.23	-2.09	2.76	1.00	827	1958
Adult females (Infant contact)	1.62	1.43	-1.25	4.38	1.00	1034	2253
Adult females (Infant OS)	1.68	3.32	-4.8	8.17	1.00	3438	2495
Adult males	2.53	1.66	-0.8	5.72	1.00	1054	1926
Juvenile-1 females	-1.98	1.59	-5.13	1.11	1.00	1375	2031
Juvenile-1 males	-2.02	1.53	-5.03	0.86	1.00	1236	2315
Juvenile-2 females	-0.71	1.47	-3.59	2.08	1.00	1301	2472
Juvenile-2 males	2.34	1.39	-0.48	5.06	1.00	965	1908
Juvenile-3 males	1.89	1.72	-1.46	5.23	1.00	1058	2242
Camp : Peripheral	2.39	3.3	-3.99	8.95	1.00	572	1308
Farm : Peripheral	1.73	4.12	-6.38	9.68	1.00	1052	1852
Forest : Peripheral	2.06	3.31	-4.31	8.53	1.00	630	1219
Grassland : Peripheral	0.94	2.84	-4.53	6.78	1.00	435	1045
Road : Peripheral	-0.46	3.17	-6.56	5.92	1.00	607	1581
Rock : Peripheral	2.77	3.43	-4.01	9.58	1.00	683	1863
Woodland : Peripheral	0.72	2.92	-4.88	6.63	1.00	528	1143
Camp : Number of neighbours	1.37	1.06	-0.69	3.54	1.00	797	1924
Farm : Number of neighbours	1.85	1.43	-1	4.65	1.00	1112	2490
Forest : Number of neighbours	1.98	1.04	-0.02	4.05	1.00	718	1612
Grassland : Number of neighbours	1.11	0.92	-0.7	2.89	1.00	606	1479
Road : Number of neighbours	1.03	1.01	-0.9	3.03	1.00	674	1469
Rock : Number of neighbours	0.77	1.01	-1.16	2.78	1.00	695	1365
Woodland : Number of neighbours	1.32	0.94	-0.51	3.16	1.00	635	1463
Camp : Time not engaged	0.15	0.18	-0.22	0.52	1.00	772	1445
Farm : Time not engaged	-0.29	0.22	-0.72	0.14	1.00	946	1867
Forest : Time not engaged	0.35	0.21	-0.07	0.77	1.00	869	1743

Grassland : Time not engaged	-0.02	0.16	-0.33	0.28	1.01	619	1169
Road : Time not engaged	0.02	0.18	-0.33	0.37	1.01	773	1538
Rock : Time not engaged	0.28	0.21	-0.12	0.7	1.00	920	1809
Woodland : Time not engaged	0.27	0.16	-0.05	0.58	1.01	639	1070
Date							
sd(Intercept)	1.99	0.38	1.22	2.74	1.00	1503	1983
ID							
sd(Intercept)	1.19	0.48	0.19	2.07	1.00	774	804
Family							
sigma	10.35	0.26	9.86	10.86	1.00	2305	2630

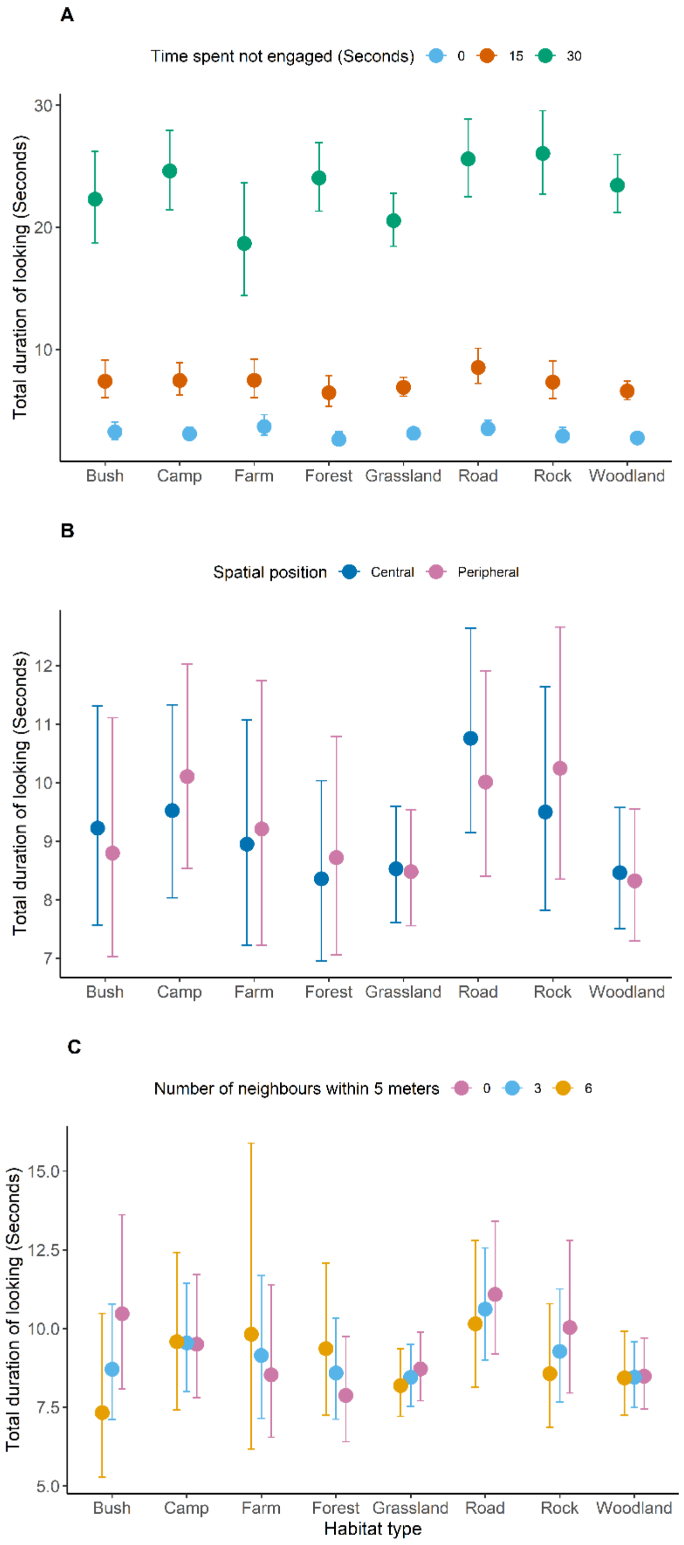

Figure S7. Conditional effects plots showing how the duration of looking bouts varied according to the interaction between habitat type and (panel A) time spent not engaged, (B) spatial position, and (C) number of neighbours within 5 meters. For time spent not engaged the conditional means and credible intervals (92.5% and 97.5% quantiles) are shown for specific values of time spent engaged (i.e., 0, 15, 30 seconds) for graphical purposes only. This was also done for number of neighbours at different values (0, 3, and 6 neighbours).

Table S18. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between home range familiarity at the location of the focal observation (inverted utilisation distribution) and several other reported risk factors, including time spent engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.25	0.1	-2.44	-2.05	1.00	1493	2456
Inverted utilisation distribution	0.04	0.09	-0.14	0.21	1.00	2553	2867
Spatial position (Peripheral)	0.06	0.03	0	0.12	1.00	3111	3212
Number of neighbours (5m)	-0.03	0.01	-0.05	-0.02	1.00	3371	3332
Time spent engaged	-0.01	0	-0.01	0	1.00	5340	3226
Rank	0	0	0	0.01	1.00	2036	3011
Visibility	0	0	0	0	1.00	4028	2836
Adolescent males	-0.3	0.11	-0.53	-0.08	1.00	1533	2641
Adult females	-0.16	0.06	-0.27	-0.05	1.00	1146	2045
Adult females (Infant contact)	-0.15	0.06	-0.28	-0.03	1.00	1370	2423
Adult females (Infant OS)	-0.05	0.12	-0.29	0.19	1.00	3402	2668
Adult males	-0.26	0.09	-0.44	-0.07	1.00	1181	1920
Juvenile-1 females	0.09	0.07	-0.06	0.23	1.00	1514	2311
Juvenile-1 males	0.02	0.08	-0.13	0.18	1.00	1298	2114
Juvenile-2 females	-0.04	0.06	-0.16	0.08	1.00	2107	2538
Juvenile-2 males	-0.05	0.07	-0.19	0.09	1.00	1092	1545
Juvenile-3 males	-0.11	0.09	-0.29	0.07	1.00	1252	2072
IUD : Peripheral	0.05	0.09	-0.11	0.23	1.00	3058	3336
IUD : Number of neighbours	0.03	0.02	-0.02	0.08	1.00	3236	3002
IUD : Time spent engaged	0.01	0	0	0.01	1.00	7150	2839
Date							
sd(Intercept)	0.17	0.02	0.14	0.21	1.00	1383	2349
ID							
sd(Intercept)	0.13	0.02	0.09	0.16	1.00	1617	2544

Table S19. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between home range familiarity at the location of the focal observation (inverted utilisation distribution) and several other reported risk factors, including time spent not engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-65.87	2.89	-71.67	-60.4	1.00	2413	2682
Inverted utilisation distribution	17.47	4.3	9.29	26.14	1.00	3689	2982
Spatial position (Peripheral)	-0.79	0.78	-2.32	0.71	1.00	4633	3480
Number of neighbours (5m)	-0.37	0.21	-0.78	0.03	1.00	4420	2785
Time spent not engaged	1.62	0.07	1.5	1.76	1.00	3244	3136
Rank	-0.01	0.02	-0.05	0.03	1.00	2887	2614
Visibility	0.14	0.02	0.11	0.18	1.00	7601	2975
Adolescent males	1.89	2	-2.06	5.8	1.00	1903	2540
Adult females	0.36	1.21	-2.02	2.75	1.00	1472	2204
Adult females (Infant contact)	1.46	1.43	-1.46	4.3	1.00	1713	2239
Adult females (Infant OS)	2.2	3.35	-4.41	8.5	1.00	4386	2856
Adult males	2.37	1.65	-0.89	5.63	1.00	1565	2162
Juvenile-1 females	-2.18	1.59	-5.28	0.93	1.00	2104	2653
Juvenile-1 males	-1.86	1.52	-4.86	1.15	1.00	1880	2538
Juvenile-2 females	-0.38	1.48	-3.36	2.47	1.00	2199	2749
Juvenile-2 males	2.38	1.33	-0.25	4.98	1.00	1579	2639
Juvenile-3 males	1.27	1.73	-2.1	4.69	1.00	1662	2668
IUD : Peripheral	-2.55	2.14	-6.61	1.62	1.00	4441	3167
IUD : Number of neighbours	-1.01	0.55	-2.06	0.07	1.00	4104	3100
IUD : Time spent not engaged	-0.49	0.15	-0.79	-0.21	1.00	4126	3230
Date							
sd(Intercept)	2.01	0.38	1.28	2.75	1.00	1617	2030
ID							
sd(Intercept)	1.2	0.47	0.18	2.05	1.00	921	1047
Family							
sigma	10.4	0.25	9.94	10.91	1.00	2549	3228

Table S20. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between home range familiarity at the location of the focal observation (core, frequently used, and boundary areas) and several other reported risk factors, including time spent engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.26	0.1	-2.47	-2.06	1.00	1455	2136
Home range familiarity (Core)	-0.07	0.05	-0.17	0.04	1.00	2231	2654
Home range familiarity (Frequent)	0.06	0.05	-0.04	0.16	1.00	2311	3091
Spatial position (Peripheral)	0.07	0.04	0	0.15	1.00	2176	2401
Number of neighbours (5m)	-0.01	0.01	-0.04	0.01	1.00	2297	3095
Time spent engaged	-0.01	0	-0.01	0	1.00	6223	3713
Rank	0	0	0	0.01	1.00	2186	2674
Visibility	0	0	0	0	1.00	4019	3013
Adolescent males	-0.31	0.11	-0.53	-0.09	1.00	1608	2879
Adult females	-0.16	0.06	-0.28	-0.05	1.00	990	2045
Adult females (Infant contact)	-0.15	0.07	-0.28	-0.02	1.00	1342	2583
Adult females (Infant OS)	-0.04	0.12	-0.29	0.19	1.00	3034	2815
Adult males	-0.27	0.09	-0.44	-0.08	1.00	1162	2043
Juvenile-1 females	0.08	0.07	-0.07	0.22	1.00	1586	1927
Juvenile-1 males	0.02	0.08	-0.13	0.17	1.00	1153	1962
Juvenile-2 females	-0.04	0.06	-0.16	0.07	1.00	1875	2461
Juvenile-2 males	-0.06	0.07	-0.19	0.08	1.00	1100	1862
Juvenile-3 males	-0.12	0.09	-0.29	0.06	1.00	1442	2332
Core : Peripheral	-0.02	0.05	-0.12	0.08	1.00	2300	2735
Frequent : Peripheral	-0.08	0.05	-0.18	0.02	1.00	2349	2380
Core : Number of neighbours	-0.03	0.02	-0.06	0	1.00	2502	2637
Frequent : Number of neighbours	-0.04	0.02	-0.07	-0.01	1.00	2559	2953
Core : Time spent engaged	-0.01	0	-0.01	0	1.00	5913	3441
Frequent : Time spent engaged	0	0	-0.01	0	1.00	6103	3141
Date							
sd(Intercept)	0.17	0.02	0.14	0.21	1.00	1478	2068
ID							
sd(Intercept)	0.12	0.02	0.09	0.16	1.00	1755	2829

Table S21. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between home range familiarity at the location of the focal observation (core, frequently used, and boundary areas) and several other reported risk factors, including time spent not engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-62.58	3.05	-68.77	-56.95	1.00	1213	2304
Home range familiarity (Core)	-14.58	2.51	-19.57	-9.73	1.00	1575	2631
Home range familiarity (Frequent)	-8.17	2.36	-12.88	-3.52	1.00	1530	2246
Spatial position (Peripheral)	-0.62	0.94	-2.41	1.27	1.00	1904	2622
Number of neighbours (5m)	-0.35	0.28	-0.9	0.19	1.00	1583	2141
Time spent not engaged	1.51	0.07	1.38	1.66	1.00	1496	2195
Rank	-0.01	0.02	-0.05	0.03	1.00	2048	2633
Visibility	0.14	0.02	0.11	0.17	1.00	4575	3411
Adolescent males	1.87	2.03	-2.2	5.91	1.00	1387	2303
Adult females	0.37	1.21	-1.96	2.73	1.00	859	1488
Adult females (Infant contact)	1.52	1.44	-1.4	4.32	1.00	1032	1585
Adult females (Infant OS)	2.64	3.25	-3.74	8.89	1.00	2598	2829
Adult males	2.36	1.63	-0.85	5.57	1.00	1002	1733
Juvenile-1 females	-2.34	1.58	-5.52	0.76	1.00	1144	1939
Juvenile-1 males	-1.95	1.55	-4.9	1.13	1.00	1045	1917
Juvenile-2 females	-0.33	1.45	-3.15	2.55	1.00	1213	1745
Juvenile-2 males	2.43	1.37	-0.28	5.16	1.00	871	1621
Juvenile-3 males	1.31	1.69	-2	4.6	1.00	1092	1850
Core : Peripheral	1.37	1.28	-1.09	3.82	1.00	2174	2825
Frequent : Peripheral	-0.06	1.31	-2.6	2.51	1.00	2186	2994
Core : Number of neighbours	0.53	0.36	-0.19	1.23	1.00	1827	2228
Frequent : Number of neighbours	0.19	0.36	-0.49	0.91	1.00	1865	2478
Core : Time spent not engaged	0.45	0.09	0.28	0.62	1.00	1798	2319
Frequent : Time spent not engaged	0.25	0.08	0.09	0.42	1.00	1651	2469
Date							
sd(Intercept)	2	0.38	1.28	2.76	1.00	1400	1922
ID							
sd(Intercept)	1.09	0.5	0.1	2.03	1.01	668	702
Family							
sigma	10.43	0.25	9.94	10.94	1.00	1908	2373

Table S22. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between probability of encountering another group (at the focal observation location) and several other reported risk factors, including time spent engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.21	0.1	-2.4	-2.02	1.00	1460	2367
Risk of encountering another group (WE)	-0.57	0.27	-1.1	-0.06	1.00	2425	2791
Spatial position (Peripheral)	0.05	0.03	0	0.11	1.00	3155	2837
Number of neighbours (5m)	-0.06	0.01	-0.08	-0.05	1.00	3286	3159
Time spent engaged	-0.01	0	-0.01	-0.01	1.00	4222	3579
Rank	0	0	0	0.01	1.00	1794	2748
Visibility	0	0	0	0	1.00	4516	3055
Adolescent males	-0.3	0.11	-0.52	-0.09	1.00	1456	2317
Adult females	-0.16	0.06	-0.28	-0.04	1.01	987	1723
Adult females (Infant contact)	-0.16	0.07	-0.28	-0.03	1.00	1229	1824
Adult females (Infant OS)	-0.05	0.12	-0.29	0.18	1.00	2684	2901
Adult males	-0.26	0.09	-0.44	-0.08	1.00	1086	1842
Juvenile-1 females	0.08	0.07	-0.07	0.22	1.00	1397	2145
Juvenile-1 males	0.02	0.08	-0.14	0.17	1.00	1196	1904
Juvenile-2 females	-0.04	0.06	-0.17	0.08	1.00	1605	2308
Juvenile-2 males	-0.05	0.07	-0.19	0.08	1.00	1029	1781
Juvenile-3 males	-0.11	0.09	-0.29	0.07	1.00	1249	1976
WE : Peripheral	-0.16	0.27	-0.68	0.36	1.00	2632	3094
WE : Number of neighbours	0.32	0.08	0.16	0.47	1.00	2765	2771
WE : Time spent engaged	0.03	0.01	0.01	0.06	1.00	4721	3189
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1.00	1432	2373
ID							
sd(Intercept)	0.12	0.02	0.09	0.16	1.00	1797	2689

Table S23. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between probability of encountering another group (at the focal observation location) and several other reported risk factors, including time spent not engaged, number of neighbours, spatial position. Also included are dominance rank of the focal animal, and visibility as these factors could influence the aforementioned relationship. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-71.46	2.91	-77.39	-65.95	1.00	3035	2824
Risk of encountering another group (WE)	23.75	12.12	-0.11	46.77	1.00	4147	2737
Spatial position (Peripheral)	-0.68	0.69	-2.08	0.63	1.00	4836	3615
Number of neighbours (5m)	0	0.18	-0.36	0.35	1.00	5068	3072
Time spent not engaged	1.77	0.07	1.65	1.91	1.00	3594	2756
Rank	-0.01	0.02	-0.05	0.03	1.00	3599	3080
Visibility	0.14	0.02	0.11	0.17	1.00	6541	3063
Adolescent males	2.32	2.07	-1.6	6.38	1.00	2377	2921
Adult females	0.46	1.22	-1.94	2.88	1.00	1855	2434
Adult females (Infant contact)	1.65	1.44	-1.22	4.42	1.00	2090	2720
Adult females (Infant OS)	2.31	3.16	-3.91	8.34	1.00	4777	2831
Adult males	2.31	1.68	-0.98	5.64	1.00	2165	2578
Juvenile-1 females	-2.09	1.62	-5.27	1.13	1.00	2571	3123
Juvenile-1 males	-1.82	1.56	-4.76	1.39	1.00	2380	3006
Juvenile-2 females	-0.28	1.44	-3.19	2.46	1.00	2658	3302
Juvenile-2 males	2.45	1.37	-0.25	5.1	1.00	1995	2515
Juvenile-3 males	1.36	1.74	-2.07	4.77	1.00	2136	2820
WE : Peripheral	8.79	7.03	-5.16	22.31	1.00	4893	3038
WE : Number of neighbours	-1.37	1.93	-5.21	2.44	1.00	4745	2828
WE : Time spent engaged	-0.44	0.41	-1.23	0.38	1.00	4544	2728
Date							
sd(Intercept)	1.99	0.37	1.27	2.74	1.00	1630	2596
ID							
sd(Intercept)	1.25	0.49	0.17	2.16	1.00	963	923
Family							
sigma	10.37	0.24	9.9	10.86	1.00	3943	3218

Table S24. Summary results for model exploring the relationship between the frequency of looking bouts and the interaction between the individual tolerance level (of the focal animal) and several other reported risk factors, including time spent engaged, observer distance, and observer movement. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-2.15	0.09	-2.32	-1.98	1.00	2591	2942
Tolerance	0.18	0.08	0.02	0.35	1.00	3677	2981
Observer distance (meters)	0.01	0.01	-0.01	0.02	1.00	4674	3722
Time spent engaged	-0.01	0	-0.02	-0.01	1.00	5930	3355
Observer movement (Yes)	0.17	0.06	0.04	0.29	1.00	5265	3091
Adolescent males	-0.44	0.1	-0.64	-0.24	1.00	2948	3401
Adult females	-0.19	0.06	-0.31	-0.08	1.00	2056	2365
Adult females (Infant contact)	-0.21	0.07	-0.34	-0.08	1.00	2245	3186
Adult females (Infant OS)	-0.08	0.12	-0.32	0.15	1.00	3588	3075
Adult males	-0.4	0.08	-0.55	-0.25	1.00	2282	2815
Juvenile-1 females	0.07	0.08	-0.07	0.22	1.00	2569	2923
Juvenile-1 males	-0.1	0.08	-0.25	0.06	1.00	1952	2364
Juvenile-2 females	-0.06	0.06	-0.19	0.06	1.00	2941	2856
Juvenile-2 males	-0.14	0.07	-0.28	0	1.00	1722	2540
Juvenile-3 males	-0.23	0.08	-0.39	-0.06	1.00	2473	2994
Tolerance : Observer distance	-0.04	0.01	-0.06	-0.02	1.00	4176	3424
Tolerance : Time spent engaged	0	0	0	0.01	1.00	6394	3403
Tolerance : Observer movement (Yes)	-0.07	0.07	-0.21	0.08	1.00	5410	2970
Date							
sd(Intercept)	0.16	0.02	0.13	0.2	1.00	1157	2459
ID							
sd(Intercept)	0.13	0.02	0.1	0.17	1.00	1556	2318

Table S25. Summary results for model exploring the relationship between the total duration of looking bouts and the interaction between the individual tolerance level (of the focal animal) and several other reported risk factors, including time spent not engaged, observer distance, and observer movement. The remainder of the population-level and group-level factors are the same as the minimal model.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-66.09	3.08	-72.32	-60.2	1.00	1962	2403
Tolerance	5.52	2.66	0.37	10.66	1.00	2666	2903
Observer distance (meters)	0.2	0.19	-0.18	0.58	1.00	3394	3333
Observer movement (Yes)	2.38	1.82	-1.27	5.92	1.00	4250	3156
Time spent not engaged	1.93	0.09	1.76	2.11	1.00	2213	2501
Adolescent males	3.17	1.82	-0.45	6.72	1.00	2368	3273
Adult females	0.46	1.27	-2.06	2.94	1.00	1395	2405
Adult females (Infant contact)	1.77	1.51	-1.22	4.76	1.00	1888	2930
Adult females (Infant OS)	2.52	3.33	-3.99	9	1.00	4461	3200
Adult males	3.66	1.39	0.9	6.33	1.00	1642	2128
Juvenile-1 females	-2.04	1.61	-5.19	1.06	1.00	1894	2490
Juvenile-1 males	-1.66	1.57	-4.74	1.39	1.00	1617	2678
Juvenile-2 females	0.04	1.5	-2.94	2.89	1.00	1904	2381
Juvenile-2 males	3.36	1.39	0.67	6.07	1.00	1427	2533
Juvenile-3 males	2.48	1.6	-0.64	5.67	1.00	1697	2599
Tolerance : Observer distance	-0.17	0.24	-0.65	0.3	1.00	3332	3184
Tolerance : Observer movement (Yes)	-1.95	2.08	-5.91	2.22	1.00	4217	3107
Tolerance : Time spent not engaged	-0.2	0.08	-0.37	-0.04	1.00	3234	3145
Date							
sd(Intercept)	2.1	0.39	1.35	2.89	1.00	1677	1986
ID							
sd(Intercept)	1.23	0.49	0.19	2.15	1.01	834	804
Family							
sigma	10.58	0.26	10.1	11.1	1.00	2882	2802

Chapter 8: Summary, conclusions, and future directions

8.1 Summary of review findings, implications of definitional variation, and future questions

Research interested in the role of vigilance in animal life dates back over a century (1). Although the initial attention concerned the adaptive benefits of group-living, more recent work has investigated a wide-range of potential functions and drivers of vigilance patterns, with particular focus on within-group threats for gregarious species (18, 143). However, a key issue that continues to plague the field is how we may identify appropriate markers for vigilance (1, 43). In some species such as birds, head-raising or head-up postures are relatively straight forward to monitor, but there is not universal agreement as to whether they are inextricably tied to vigilance use (27). This subject matter is even more complex in mammalian (and particularly primate) species as animals can use their hands whilst looking around (15, 144). In addition, to these factors, there is not a clear agreement as to whether vigilance must be tied to threat detection or monitoring, or whether it has been expanded to incorporate other functions of general looking behaviours (43).

In chapter 2 (43), I found numerous ethoses had emerged within primate vigilance research, potentially as a result of some of the aforementioned challenges. In my third chapter I found evidence that different definitions may produce important differences in results, i.e., definition effects. I also found that some definitions are more challenging for different observers to reach agreement on, and that these differences in interpretation can ultimately lead to differences in results, i.e., interpretation effects. Although vigilance is a complex behaviour to monitor, a variety of other behaviours also pose unique challenges for observers to agree on. Our results indicate that definitions must be well-defined and operationalised, but even then, can still produce varied results. These findings transcend arguments about the true meaning and function of vigilance and present several concerns for behavioural ecologists to consider going forward - what is the extent of definitional and methodological variation for other behaviours? Are there inconsistencies within species and taxa? And if so, does variation pose a problem for making reliable cross-study, population, and species comparisons?

8.2 Summary of tolerance findings

My review of primate vigilance literature also highlighted that few authors appeared to consider nor control for the presence and behaviour of researchers during direct observations on habituated subjects (43). Indeed, this may be a factor that transcends numerous research themes in behavioural ecology. In my fourth chapter I was able to use FID approach methods to produce individual tolerance estimates for each member of the habituated group of baboons at Lajuma. As part of this, we observed that the baboons were always displaced by our approaches and acted in a very benign and passive manner whilst moving away. Such responses are akin to scenarios where subordinate baboons are displaced by dominant individuals, which may suggest the study group viewed the researchers as equivalent to social threats. Collectively, these results suggested that researchers were not considered neutral and that individual baboons varied in their tolerance of researchers (145). Additionally, we validated that these individual estimates were consistent even after a predation event by a leopard (chapter 5), suggesting the baboons had a very specific perception of researchers during observations, and that the individuality of tolerance is unlikely to be variable when observations are consistent through time. Such results have important implications for many research themes which we explored in more detail in the remaining chapters.

8.3 The implications of tolerance for research using direct observation on habituated study subjects

The first implication of individual-level tolerance differences is that researchers may influence the space use of group members, specifically, it is likely that intolerant individuals avoid being in proximity to researchers. In chapter 6, I used data collected on inter-individual proximity patterns of the habituated group and found that very intolerant individuals clearly avoided proximity of the observer. The implications of this finding suggest it is possible for researchers to bias the inter-observer proximity data they record, especially if tolerance factors and observer distances are not considered. There are examples where researchers have circumnavigated these issues by removing intolerant animals from their social network analyses (e.g., (146)); however, this strategy does not remove the possibility of researchers affecting the movement of these individuals. In addition, removing individuals based on phenotype (as opposed to a random process) will likely bias data and create networks that are different from reality (146, 147).

Although many experienced researchers are likely innately aware of such factors, and simply increasing observation distances is an adequate strategy in most cases (especially in open environments). It may however be impossible to eradicate these issues entirely, especially in environments dominated by dense vegetation where researchers need to observe from closer distances. In addition, not all studies can undertake observations on animals that have been under direct observation for multiple years, in many cases the animals are likely still undergoing habituation processes when data collection commences, such scenarios are most at risk of observer-effects on animal behaviour. Thus, tolerance related observer-effects should be discussed more frequently in studies using direct observations of habituated subjects, with individual tolerance levels estimated and included as a crucial component of research methodologies.

8.3.1 Study limitations and future tolerance questions

Although we found individual consistency in both visual orientation distance and flight initiation distance in the study group, future work needs to explore additional methods to ensure convergent validity requirements are met, and investigate discriminate validity with other traits such as boldness, both are required to confirm whether tolerance is an independent personality trait (85). Although boldness may be the most likely trait to overlap with tolerance, it is necessary to also explore whether individuals vary in their preference for space and proximity to other animals (148). For example, it may be necessary to demonstrate that individual baboons also have varied tolerances of one-another, and that their tolerance of observers is distinguishable from these underlying patterns of behaviour. In addition, it is unlikely that researchers will be able to approach their study subjects without fear of retaliation at all study sites, as such, researchers should explore whether non-approach methods can be used to assess observer tolerance.

At present little work has explored the landscape level consequences of habituated study groups on the other animals that they share space with. For example, habituated baboon groups may be better able to displace unhabituated baboon groups from contestable resources when a researcher is present, as the unhabituated animals will likely view the researcher as equivalent to a predator (93). Similarly, it seems likely that researchers act as a human-shield (69) and may scare natural predators away from the group, leading to artificially low predation rates, which can consequently lead to bigger group sizes and further alter the competition dynamics with other animals occupying the area. The dynamics and implications of these processes require urgent research attention, especially in areas where predator species are at low densities.

8.5 Summary of findings for questions exploring the key predictors of looking

In my final chapter I explored the key predictors of looking in the study group of baboons at Lajuma, utilising the definition I presented in chapter 2 (43), which I found the most support for in chapter 3. The most common approach to studying vigilance patterns is to explore a small number of vigilance drivers in isolation, thus allowing researchers to focus in on specific hypotheses. This has proved popular in primatology as researchers often elect to sample the subtypes of vigilance directly, e.g., antipredator, social, reactionary, preemptive (43); however, by utilising the proposed looking framework I was able to explore a more complete list of risk, behavioural, and compatibility hypotheses in tandem and explore their relative weighting to one another (149, 150).

My results highlighted that the baboons at Lajuma were particularly sensitive to ongoing encounters with other groups (elevated duration and frequency of looking bouts) and also attentive to when their local social environment became riskier, i.e., they elevated looking patterns in response to increasing numbers of threatening group-members being nearby. We also found some evidence supporting preemptive vigilance hypotheses for other threats, for example, individuals on the periphery of the group increased looking when on farms, indicating the group held some fear of local humans despite generally tolerating researchers (145).

Interestingly, the study group's looking patterns were not consistently explained by the interaction between individual tolerance estimates and the proximity and behaviour of researchers. This finding adds some validity to my results but may also demonstrate that when aware of tolerance factors, researchers can adjust their behaviour accordingly (e.g., increase observation distances for intolerant individuals), thus achieving the goal of having minimal influence on the behaviours we record. It also highlights that concentrating purely on focal animals as a barometer for observer-effects is inadequate, as across the same focal observations we showed that when the observer was within 4.5 meters (of a focal animal) that intolerant animals were less likely to occur in proximity and make physical contact with the focal animal.

Despite finding some support for preemptive and reactionary risk drivers of looking, I found that the study animals consistently performed looking behaviours whenever their underlying behaviour afforded the opportunity to do so. For example, certain food items required repeated bites during processing, which were often accompanied with brief looks. Although this may be considered tantamount to routine vigilance (e.g., (22)), there is no indication the baboons routinely interrupted their behaviour to look around; rather they appear to exhibit a high propensity for utilising compatible moments of looking time during their engaged behaviours. The fact that these episodes rarely overlapped with spatial predictors of risk (e.g., likelihood of encountering a leopard or other baboon groups) suggests it may simply be an innate behaviour as opposed to a conscious monitoring decision, i.e., routine vigilance. I found that the baboons detected approaches made by researchers rapidly and this ability was not substantially inhibited by engagement in complex foraging tasks (145). Combined, these results may suggest the group at Lajuma have little need to be proactively vigilant in locations associated with higher risk of encountering a threat and can instead rely on their innate habits and their sensory capacity to detect threats if they are present.

8.5.1 Study limitations, ongoing methodological considerations, and future questions

These results could also pose an important argument concerning the construction of landscapes of fear. In chapter 7, I utilised long term encounter data to create spatial layers predicting the likelihood of baboons encountering threats from other groups. These methods are similar to those utilised for constructing landscapes of fear for various threats in vervet monkeys and samangos at the study site (151–153). One improvement was that I utilised a scale-integration of 2nd and 3rd order resource selection functions (154), derived from GPS collar data from leopards at the Lajuma study site (138). This spatial layer should have therefore been an excellent proxy for the true likelihood of a baboon encountering a leopard at their location during a focal observation. However, there was little evidence to suggest the looking behaviours of the study group were sensitive to the spatial likelihood of encountering other groups or leopards. It may be that other behaviours are sensitive to spatial risk on these scales, for example, individuals may reduce their inter-individual distances (i.e., become more cohesive) in areas of higher risk instead (153).

It is also debateable whether baboons should be sensitive to such complex information concerning the true likelihood of encountering these threats, or instead rely on spatial memory of recent or historical encounters to inform their risk sensitive behaviours. For example, the baboons may instead exhibit short term avoidance of areas after negative experiences, instead of acting pre-emptively in areas with the greatest likelihood of threats occurring. Conversely, the baboon's landscape of fear could be more nuanced, and most sensitive to climatic conditions and how these interact with predator behaviour, e.g., misty conditions reduce visibility, whilst being associated with increased leopard activity at Lajuma (138). Finally, although I included habitat visibility and habitat type as hypotheses in chapter 7, both may overlook the specific information that determines the baboon's perception of risk. For example, the interaction between visibility, refuge availability, and proximity to farms may be more important than the proximity of the farm itself.

Future work would benefit from exploring the response of several hypothesized risk-sensitive behaviours within the same study, allowing their relative contributions to antipredator behaviour to be weighted effectively. In addition, for each predator and external threat, these landscapes of fear should be constructed across various timescales and conditions. This should help elucidate important information about how animals perceive risk innately, the extent with which they can learn and adjust behaviours from experience, and the duration and extent of their spatial memory for threats. Ultimately, with so many environmental and social stimuli available for the baboons to be attentive to, vigilance and indeed looking behaviours are unlikely to consistently be the most risk-sensitive behaviours in pre-emptive scenarios.

Although the construction and use of the looking definition was supported from detailed analyses that have not been used in primatology before, we found that no definition was immune to definition and interpretation effects. This is therefore an important limitation of our findings, and we strongly recommend that future researchers strive towards a conclusion to the debate regarding defining vigilance and the specific markers that are required to sample its use. Despite this, we found support for numerous vigilance hypotheses despite making no attempt to sample vigilance directly. Future research may benefit from exploring this approach if it is agreed that consolidation on methodological approaches is necessary.

8.6 Conclusion

In conclusion, in investigating a well-studied behaviour (i.e., vigilance), I uncovered numerous methodological inconsistencies and factors that had received minimal research attention. Although I made attempts to find solutions to methodological variation, it is impossible for a single study to tackle alone, especially when similar concerns are likely to be present for other behaviours and across numerous taxa. This thesis highlights that small sources of variation can lead to clear differences in results, and that overlooked phenomena (e.g., tolerance) can bias the data that researchers collect. It is important that future research utilising direct observations does not shy away from these findings and instead sees the fruitful opportunities in exploring their implications and developing clear strategies for consolidating research methods going forward.

References for chapters 1 (Thesis introduction) and 8 (Summary, conclusions, and future directions)

1. G. Beauchamp, *Animal vigilance: monitoring predators and competitors* (Academic Press, 2015).

2. I. Vine, Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* **30**, 405–422 (1971).

3. W. D. Hamilton, Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311 (1971).

4. H. R. Pulliam, On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422 (1973).

5. G. V. N. Powell, Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**, 501–505 (1974).

6. R. C. Miller, The significance of the gregarious habit. *Ecology* **3**, 122–126 (1922).

7. M. M. Dehn, Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**, 337–342 (1990).

8. J. M. McNamara, A. I. Houston, Evolutionarily stable levels of vigilance as a function of group size. *Anim. Behav.* **43**, 641–658 (1992).

9. G. Roberts, Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086 (1996).

10. M. Elgar, Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**, 13–33 (1989).

11. S. L. Lima, Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20 (1995).

12. H. R. Pulliam, G. H. Pyke, T. Caraco, The scanning behavior of juncos: A game-theoretical approach. *J. Theor. Biol.* **95**, 89–103 (1982).

13. R. S. Olson, P. B. Haley, F. C. Dyer, C. Adami, R. S. Olson, Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *R. Soc. Open Sci.* **2**, 150135 (2015).

14. A. Treves, Theory and method in studies of vigilance and aggregation. *Anim. Behav.* **60**, 711–722 (2000).

15. G. Cowlishaw, *et al.*, A simple rule for the costs of vigilance: empirical evidence from a social forager. *Proc. R. Soc. B Biol. Sci.* **271**, 27–33 (2004).

16. D. J. Baker, R. A. Stillman, S. L. Smart, J. M. Bullock, K. J. Norris, Are the costs of routine vigilance avoided by granivorous foragers? *Funct. Ecol.* **25**, 617–627 (2011).

17. C. . van Shaik, M. . van Noordwijk, The special role of male Cebus monkeys in predation avoidance and its effect on group composition. *Behav. Ecol. Sociobiol.* **24**, 265–276 (1989).

18. N. Kutsukake, The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology* **112**, 581–591 (2006).

19. K. M. Gaynor, M. Cords, Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Anim. Behav.* **84**, 531–537 (2012).

20. N. Kazahari, N. Agetsuma, Mechanisms determining relationships between feeding group size and foraging success in food patch use by Japanese macaques (*Macaca fuscata*). *Behaviour*

147, 1481–1500 (2010).

21. A. D. Gosselin-Ildari, A. Koenig, The Effects of Group Size and Reproductive Status on Vigilance in Captive *Callithrix jacchus*. *Am. J. Primatol.* **74**, 613–621 (2012).

22. P. Blanchard, H. Fritz, Induced or routine vigilance while foraging. *Oikos* **116**, 1603–1608 (2007).

23. J. A. Teichroeb, P. Sicotte, Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behav. Ecol. Sociobiol.* **66**, 453–466 (2012).

24. S. U. E. Boinski, *et al.*, Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis, S. sciureus*). *Behaviour* **139**, 1421–1467 (2003).

25. A. J. J. MacIntosh, P. Sicotte, Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): An examination of the effects of conspecific threat and predation. *Am. J. Primatol.* **71**, 919–927 (2009).

26. L. Gould, Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Int. J. Primatol.* **17**, 331–347 (1996).

27. K. Tatte, J. D. Ibanez-Alamo, G. Marko, R. Mand, A. P. Moller, Antipredator function of vigilance re-examined : vigilant birds delay escape b. *Anim. Behav.* **156**, 97–110 (2019).

28. M. Cords, Predator Vigilance Costs of Allogrooming in Wild Blue Monkeys. *Behaviour* **132**, 559–569 (1995).

29. N. G. Caine, S. L. Marra, Vigilance and social organization in two species of primates. *Anim. Behav.* **36**, 897–904 (1988).

30. L. M. Rose, L. M. Fedigan, Vigilance in white-faced capuchins, *Cebus capuchinus*, in Costa Rica. *Anim. Behav.* **49**, 63–70 (1995).

31. Oxford University Press, Vigilance - definition of vigilance in English | Oxford Dictionaries. *Lexico.com* (2019) (December 4, 2019).

32. F. Galton, Gregariousness in cattle and in men. *Macmillan's Mag.* **23**, 353–57 (1871).

33. S. Dimond, J. Lazarus, The problem of vigilance in animal life. *Brain. Behav. Evol.* **9**, 60–79 (1974).

34. L.-A. Giraldeau, T. Caraco, *Social Foraging Theory* (Princeton University Press, 2000).

35. K. R. L. Hall, Social vigilance behaviour of the chacma baboon, Papio ursinus. *Behaviour* **16**, 261–293 (1960).

36. D. W. Jenkins, Territory as a result of despotism and social organization in geese. *Auk* **61**, 30–47 (1944).

37. J. Burger, M. Gochfeld, Effects of group size and sex on vigilance in ostriches (*Stuthio camelus*): Antipredator strategy or mate competition? *Ostrich J. African Ornithol.* **59**, 14–20 (1988).

38. K. R. L. Hall, Numerical Data, Maintenance Activities and Locomotion of the Wild Chacma Baboon, *Papio Ursinus*. *Proc. Zool. Soc. London* **139**, 181–220 (1962).

39. G. Hausfater, D. Takacs, Structure and Function of Hindquarter Presentations in Yellow Baboons (*Papio cynocephalus*). *Ethology* **74**, 297–319 (1987).

40. T. Mueller, W. F. Fagan, V. Grimm, Integrating individual search and navigation behaviors in mechanistic movement models. *Theor. Ecol.* **4**, 341–355 (2011).

41. E. S. Cameron, Observations on the golden eagle in Montana. *Auk* **XXV**, 251–268 (1908).

42. P. H. T. Hartley, Review : Predation by sparrow-hawk populations. *Ecology* **28**, 326–328 (1947).

43. A. T. L. Allan, R. A. Hill, What have we been looking at? A call for consistency in studies of primate vigilance. *Am. J. Phys. Anthropol.* **165**, 4–22 (2018).

44. A. Treves, The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour* **135**, 453–481 (1998).

45. M. Baldellou, P. S. Henzi, Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Anim. Behav.* **43**, 451–461 (1992).

46. J. R. de Ruiter, The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour* **98**, 240–258 (1986).

47. D. Fragaszy, Sex and age differences in the organisation of behaviour in wedge-capped capuchins, *Cebus olivaceus*. *Behav. Ecol.* **1**, 81–94 (1990).

48. L. Gould, L. M. Fedigan, L. M. Rose, Why Be Vigilant? The Case of the Alpha Animal. *Int. J. Primatol.* **18**, 401–414 (1997).

49. L. A. Isbell, T. P. Young, Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav. Ecol. Sociobiol.* **32**, 377–385 (1993).

50. A. Treves, Vigilance and Spatial Cohesion among Blue Monkeys. *Folia Primatol.* **70**, 291–294 (1999).

51. A. Treves, A. Drescher, C. T. Snowdon, Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology* **109**, 135–146 (2003).

52. R. Steenbeek, R. C. Piek, M. van Buul, J. A. R. A. M. van Hooff, Vigilance in wild Thomas's langurs (*Presbytis thomasi*): The importance of infanticide risk. *Behav. Ecol. Sociobiol.* **45**, 137–150 (1999).

53. A. Treves, Within-group vigilance in red colobus and redtail monkeys. *Am. J. Primatol.* **48**, 113–126 (1999).

54. K. Onishi, M. Nakamichi, Maternal Infant Monitoring in a Free-ranging Group of Japanese Macaques (*Macaca fuscata*). *Int. J. Primatol.* **32**, 209–222 (2011).

55. A. Treves, A. Drescher, N. Ingrisano, Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behav. Ecol. Sociobiol.* **50**, 90–95 (2001).

56. K. K. Watson, *et al.*, Genetic influences on social attention in free-ranging rhesus macaques. *Anim. Behav.* **103**, 267–275 (2015).

57. G. Cowlishaw, The role of vigilance in the survival and reproductive strategies of Desert Baboons. *Behaviour* **135**, 431–452 (1998).

58. M. Stojan-Dolar, E. W. Heymann, Vigilance in a cooperatively breeding primate. *Int. J. Primatol.* **31**, 95–116 (2010).

59. L. Busia, C. M. Schaffner, F. Aureli, Watch out or relax: conspecifics affect vigilance in wild spider monkeys (*Ateles geoffroyi*). *Behaviour* **153**, 107–124 (2016).

60. D. P. Watts, A preliminary study of selective visual attention in female mountain gorillas (*Gorilla gorilla beringei*). *Primates* **39**, 71–78 (1998).

61. M. Cords, Vigilance and mixed-species associations of some East African forest monkeys. *Behav. Ecol. Sociobiol.* **26**, 297–300 (1990).

62. S. C. Alberts, Vigilance in young baboons: effects of habitat, age, sex and maternal rank on glance rate. *Anim. Behav.* **47**, 749–755 (1994).

63. R. A. Hill, G. Cowlishaw, “Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations” in *Eat or Be Eaten: Predator Sensitive Foraging Among Primates*, L. E. Miller, Ed. (Cambridge University Press, 2002), pp. 187–204.

64. A. C. Smith, S. Kelez, H. M. Buchanan-Smith, Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). *Behav. Ecol. Sociobiol.* **56**, 18–25 (2004).

65. J. G. Robinson, Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. *Anim. Behav.* **29**, 1036–1056 (1981).

66. A. Treves, Primate Social Systems: Conspecific Threat and Coercion-Defense Hypotheses. *Folia Primatol.* **69**, 81–88 (1998).

67. C. L. Hall, L. M. Fedigan, Spatial benefits afforded by high rank in white-faced capuchins. *Anim. Behav.* **53**, 1069–1082 (1997).

68. A. Treves, K. Brandon, “Tourist impacts on the behavior of black howler monkeys (*Alouatta pigra*) at Lamanai, Belize” in *Commensalism and Conflict: The Human-Primate Interface*, (2005), pp. 147–167.

69. K. Nowak, A. Le Roux, S. A. Richards, C. P. J. Scheijen, R. A. Hill, Human observers impact habituated samango monkeys’ perceived landscape of fear. *Behav. Ecol.* **25**, 1199–1204 (2014).

70. D. M. Nunes, I. Gonçalves, N. Emile, M. Barros, Bimodal temporal organization of specific vigilance behaviors in captive black tufted-ear marmosets (*Callithrix penicillata*). *Behav. Processes* **84**, 629–631 (2010).

71. M. Barros, C. Alencar, M. A. de S. Silva, C. Tomaz, Changes in experimental conditions alter anti-predator vigilance and sequence predictability in captive marmosets. *Behav. Processes* **77**, 351–356 (2008).

72. N. G. Caine, Visual scanning by tamarins. *Folia Primatol.* **43**, 59–67 (1984).

73. P. L. Pannozzo, K. A. Phillips, M. E. Haas, E. M. Mintz, Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (*Cebus apella*). *Ethology* **113**, 881–888 (2007).

74. A. Koenig, Visual Scanning by Common Marmosets (*Callithrix jacchus*): Functional Aspects and the Special Role of Adult Males. *Primates* **39**, 85–90 (1998).

75. D. T. Blumstein, Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.* **120**, 255–262 (2016).

76. C. H. Rankin, *et al.*, Habituation revisited: An updated and revised description of the

behavioral characteristics of habituation. *Neurobiol. Learn. Mem.* **92**, 135–138 (2008).

77. L. M. Fedigan, Ethical issues faced by field primatologists: Asking the relevant questions. *Am. J. Primatol.* **72**, 754–771 (2010).

78. L. Bejder, A. Samuels, H. Whitehead, H. Finn, S. Allen, Impact assessment research: Use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* **395**, 177–185 (2009).

79. E. A. Williamson, A. T. C. Feistner, "Habituating primates: Processes, techniques, variables and ethics" in *Field and Laboratory Methods in Primatology: A Practical Guide, Second Edition*, J. M. Setchell, D. J. Curtis, Eds. (Cambridge University Press, 2011), pp. 33–50.

80. K. M. Jack, *et al.*, The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am. J. Primatol.* **70**, 490–494 (2008).

81. P. McDougall, Is passive observation of habituated animals truly passive? *J. Ethol.* **30**, 219–223 (2012).

82. M. C. Crofoot, T. D. Lambert, R. Kays, M. C. Wikelski, Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Anim. Behav.* **80**, 475–480 (2010).

83. P. Bertolani, C. Boesch, Habituation of wild chimpanzees (*Pan troglodytes*) of the south group at Taï Forest, Côte d'Ivoire: Empirical measure of progress. *Folia Primatol.* **79**, 162–171 (2008).

84. D. T. Blumstein, D. S. M. Samia, T. Stankowich, W. E. Cooper, "Best practice for the study of escape behavior" in *Escaping from Predators: An Integrative View of Escape Decisions*, W. E. Cooper, D. T. Blumstein, Eds. (Cambridge University Press, 2015), pp. 405–419.

85. A. J. Carter, W. E. Feeney, H. H. Marshall, G. Cowlishaw, R. Heinsohn, Animal personality: What are behavioural ecologists measuring? *Biol. Rev.* **88**, 465–475 (2013).

86. R. C. Ydenberg, L. M. Dill, The Economics of Fleeing form Predators. *Adv. study Behav.* **16**, 229–249 (1986).

87. W. E. Cooper, W. G. Frederick, Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67 (2007).

88. W. E. Cooper, Variation in Escape Behavior among Individuals of the Striped Plateau Lizard Sceloporus virgatus May Reflect Differences in Boldness. *J. Herpetol.* **43**, 495–502 (2009).

89. W. E. Cooper, D. S. M. Samia, D. T. Blumstein, FEAR, spontaneity, and artifact in economic escape theory: A review and prospectus. *Adv. Study Behav.* **47**, 147–179 (2015).

90. W. E. Cooper, W. G. Frederick, Predator lethality, optimal escape behavior, and autotomy. *Behav. Ecol.* **21**, 91–96 (2010).

91. S. Dalesman, C. J. Inchley, Interaction between Olfactory and Visual Cues Affects Flight Initiation and Distance by the Hermit Crab , *Pagurus bernhardus*. *Behaviour* **145**, 1479–1492 (2008).

92. A. M. Scarratt, J.-G. J. Godin, Foraging and antipredator decisions in the hermit crab *Pagurus acadianus* (Benedict). *J. Exp. Mar. Bio. Ecol.* **156**, 225–238 (1992).

93. A. Frid, L. M. Dill, Human-caused disturbance stimuli as a form of predation risk. *Ecol. Soc.* **6**, 11 (2002).

94. M. Díaz, *et al.*, The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape Distances of Birds across Europe. *PLoS One* **8**, e64634 (2013).

95. T. Stankowich, D. T. Blumstein, Fear in animals: A meta-analysis and review of risk assessment. *Proc. R. Soc. B Biol. Sci.* **272**, 2627–2634 (2005).

96. D. S. M. Samia, F. Nomura, D. T. Blumstein, Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* **9**, 1–4 (2013).

97. P. W. Bateman, P. A. Fleming, Who are you looking at? Hadeda ibises use direction of gaze, head orientation and approach speed in their risk assessment of a potential predator. *J. Zool.* **285**, 316–323 (2011).

98. W. E. Cooper, R. A. Pyron, T. Garland, Jr., Island tamesess. Living on islands reduces flight iniation distance. *Proc. R. Soc. B Biol. Sci.* **281**, 20133019 (2014).

99. W. E. Cooper, Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology* **109**, 617–626 (2003).

100. E. Fernández-Juricic, M. P. Venier, D. Renison, D. T. Blumstein, Sensitivity of wildlife to spatial patterns of recreationist behavior: A critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biol. Conserv.* **125**, 225–235 (2005).

101. A. P. Møller, P. Tryjanowski, Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behav. Ecol.* **25**, 960–966 (2014).

102. L. M. Dill, R. Houtman, The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.* **67**, 233–235 (1989).

103. P. J. Guay, R. D. A. Lorenz, R. W. Robinson, M. R. E. Symonds, M. A. Weston, Distance from Water, Sex and Approach Direction Influence Flight Distances Among Habituated Black Swans. *Ethology* **119**, 1–7 (2013).

104. K. M. Gotanda, K. Turgeon, D. L. Kramer, Body size and reserve protection affect flight initiation distance in parrotfishes. *Behav. Ecol. Sociobiol.* **63**, 1563–1572 (2009).

105. S. C. Engelhardt, R. B. Weladji, Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can. J. Zool.* **89**, 823–830 (2011).

106. D. Hawlena, V. Pérez-Mellado, W. E. Cooper, Morphological traits affect escape behaviour of the Balearic lizards (*Podarcis lilfordi*). *Amphib. Reptil.* **30**, 587–592 (2009).

107. K. Tätte, A. P. Møller, R. Mänd, Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Anim. Behav.* **136**, 75–86 (2018).

108. D. T. Blumstein, Moving to suburbia: Ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeogr.* **29**, 685–692 (2002).

109. L. A. Ikuta, D. T. Blumstein, Do fences protect birds from human disturbance? *Biol. Conserv.* **112**, 447–452 (2003).

110. E. Fernández-Juricic, *et al.*, Relationships of anti-predator escape and post-escape responses with body mass and morphology: A comparative avian study. *Evol. Ecol. Res.* **8**, 731–752 (2006).

111. A. M. Runyan, D. T. Blumstein, Do individual differences influence initiation distance? *J. Wildl. Manage.* **68**, 1124–1129 (2004).

112. F. Dumont, C. Pasquaretta, D. Réale, G. Bogliani, A. von Hardenberg, Flight Initiation Distance and Starting Distance: Biological Effect or Mathematical Artefact? *Ethology* **118**, 1051–1062 (2012).

113. F. A. Januchowski-Hartley, K. L. Nash, R. J. Lawton, Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. *Mar. Ecol. Prog. Ser.* **469**, 113–119 (2012).

114. W. E. Cooper, T. Stankowich, Prey or predator? Body size of an approaching animal affects decisions to attack or escape. *Behav. Ecol.* **21**, 1278–1284 (2010).

115. P. J. Guay, *et al.*, Observer effects occur when estimating alert but not flight-initiation distances. *Wildl. Res.* **40**, 289–293 (2013).

116. N. C. Bonnot, *et al.*, Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. *Anim. Behav.* **124**, 35–46 (2017).

117. D. T. Blumstein, Flush early and avoid the rush: A general rule of antipredator behavior? *Behav. Ecol.* **21**, 440–442 (2010).

118. D. S. M. Samia, D. T. Blumstein, Phi index: A new metric to test the flush early and avoid the rush hypothesis. *PLoS One* **9**, e113134 (2014).

119. M. B. Petelle, D. E. McCoy, V. Alejandro, J. G. A. Martin, D. T. Blumstein, Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**, 1147–1154 (2013).

120. M. Carrete, J. L. Tella, Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**, 167–170 (2010).

121. M. Carrete, J. L. Tella, High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Sci. Rep.* **3**, 1–7 (2013).

122. A. P. Møller, Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* **27**, 1105–1113 (2014).

123. A. J. Carter, R. Heinsohn, A. W. Goldizen, P. A. Biro, Boldness, trappability and sampling bias in wild lizards. *Anim. Behav.* **83**, 1051–1058 (2012).

124. J. S. Strong, R. B. Weladji, Ø. Holand, K. H. Røed, M. Nieminen, Personality and fitness consequences of flight initiation distance and mating behavior in subdominant male reindeer (*Rangifer tarandus*). *Ethology* **123**, 484–492 (2017).

125. F. I. Martinez, *et al.*, A missing piece of the Papio puzzle: Gorongosa baboon phenostructure and intrageneric relationships. *J. Hum. Evol.* **130**, 1–20 (2019).

126. S. R. Leigh, J. M. Cheverud, Sexual dimorphism in the baboon facial skeleton. *Am. J. Phys. Anthropol.* **84**, 193–208 (1991).

127. S. P. Henzi, J. E. Lycett, S. E. Piper, Fission and troop size in a mountain baboon population. *Anim. Behav.* **53**, 525–535 (1997).

128. T. S. Hoffman, M. J. O'Riain, The Spatial Ecology of Chacma Baboons (*Papio ursinus*) in a Human-modified Environment. *Int. J. Primatol.* **32**, 308–328 (2011).

129. T. J. Bergman, J. C. Beehner, D. L. Cheney, R. M. Seyfarth, Hierarchical Classification by Rank and Kinship in Baboons. *Science (80-.).* **302**, 1234–1236 (2003).

130. A. L. Engh, *et al.*, Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Anim. Behav.* **71**, 1227–1237 (2006).

131. R. M. Sapolsky, Why should an aged male baboon ever transfer troops? *Am. J. Primatol.* **39**, 149–157 (1996).

132. T. Weingrill, Infanticide and the value of male-female relationships in mountain chacma baboons. *Behaviour* **137**, 337–359 (2000).

133. S. C. Strum, Agonistic Dominance in Male Baboons: An Alternative View. *Int. J. Primatol.* **3**, 175–202 (1982).

134. T. H. C. Mostert, G. J. Bredenkamp, C. Verwey, R. E. Mostert, N. Hahn, Major Vegetation Types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *KOEDOE* **50**, 32–48 (2008).

135. K. S. Williams, S. T. Williams, L. E. Fitzgerald, E. C. Sheppard, R. A. Hill, Brown hyaena and leopard diets on private land in the Soutpansberg Mountains , South Africa. *Afr. J. Ecol.* **56**, 1021–1027 (2018).

136. J. N. Chase Grey, S. Bell, R. A. Hill, Leopard diets and landowner perceptions of human wildlife conflict in the Soutpansberg Mountains , South Africa. *J. Nat. Conserv.* **37**, 56–65 (2017).

137. G. Cowlishaw, Vulnerability to predation in baboon populations. *Behaviour* **131**, 293–304 (1994).

138. A. M. Ayers, "The behavioural ecology and predator-prey interactions of leopards (Panthera pardus) and chacma baboons (*Papio ursinus*) in an Afromontane environment," Durham University. (2019).

139. D. M. Kitchen, D. L. Cheney, R. M. Seyfarth, Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). *Behaviou* **141**, 197–218 (2004).

140. G. Cowlishaw, Behavioural Patterns in Baboon Group Encounters: The Role of Resource Competition and Male Reproductive Strategies. *Behaviour* **132**, 75–86 (1995).

141. W. J. Hamilton III, R. E. Buskirk, W. H. Buskirkt, Defense of Space and Resources by Chacma (*Papio Ursinus*) Baboon Troops in an African Desert and Swamp. *Ecology* **57**, 1264–1272 (1976).

142. A. M. Ayers, A. T. L. Allan, R. A. Hill, Foraging in fear: spatial variation in range use, vigilance, and perceived risk in chacma baboons (*Papio ursinus*). *Rev.*

143. E. Z. Cameron, J. T. Du Toit, Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Anim. Behav.* **69**, 1337–1344 (2005).

144. I. J. Makowska, D. L. Kramer, Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. *Anim. Behav.* **74**, 153–158 (2007).

145. A. T. L. Allan, A. L. Bailey, R. A. Hill, Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Sci. Adv.* **6**, eaaz0870 (2020).

146. P. Fedurek, J. Lehmann, The effect of excluding juveniles on apparent adult olive baboons (*Papio anubis*) social networks. *PLoS One* **12**, e0173146 (2017).

147. J. A. Smith, J. Moody, J. H. Morgan, Network sampling coverage II: The effect of non-random missing data on network measurement. *Soc. Networks* **48**, 78–99 (2017).

148. D. Réale, S. M. Reader, D. Sol, P. T. McDougall, N. J. Dingemanse, Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318 (2007).

149. S. Creel, P. Schuette, D. Christianson, Effects of predation risk on group size, vigilance, and

foraging behavior in an African ungulate community. *Behav. Ecol.* **25**, 773–784 (2014).

150. K. P. Burnham, D. R. Anderson, K. P. Huyvaert, AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35 (2011).

151. E. P. Willems, R. A. Hill, Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology* **90**, 546–555 (2009).

152. B. T. Coleman, R. A. Hill, Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Anim. Behav.* **88**, 165–173 (2014).

153. L. R. LaBarge, A. T. L. Allan, C. M. Berman, S. W. Margulis, R. A. Hill, Reactive and pre-emptive spatial cohesion in a social primate. *Anim. Behav.* **163**, 115–126 (2020).

154. R. T. Pitman, *et al.*, Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. *J. Appl. Ecol.* **54**, 1687–1698 (2017).

Appendices: Other published work

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Illuminating movement? Nocturnal activity patterns in chacma baboons

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Abstract

Recent analyses have shown that typically diurnal primates may periodically exhibit some levels of activity at night. Despite this, there have been few studies that have explored whether diurnal primates living in temperate environments will extend their activity budgets to the nocturnal phase as a response to seasonal constraints. Using dual-axis accelerometers, we explored whether chacma baboons (*Papio ursinus*; $N = 3$) in the western Soutpansberg Mountains, South Africa, responded to seasonally fluctuating levels of day length, lunar illumination, wind speed, precipitation and temperature by heightening or lowering nocturnal activity levels. Our results showed that chacma baboons engaged in low levels of activity at night throughout the year. Although baboons had heighted nocturnal activity as a response to shorter days, moonlit nights and lower temperatures, these responses were most likely due to disturbed sleeping patterns rather than more active movement. Nocturnal activity significantly dropped in a female baboon throughout the course of her pregnancy and remained low after giving birth suggesting that females with infants must increase resting. Our results compliment previous analyses which suggest that although diurnal primates may periodically be active at night, there is limited evidence for strategic use of the nocturnal phase even in highly seasonal environments.

Introduction

Diel activity patterns typically refer to when a species is primarily active. While most mammals are active at night (nocturnal), several taxa have evolved to be active during daylight hours only (diurnal), at intermediate light conditions (such as at dawn and dusk: crepuscular) or throughout the 24-h cycle (cathemeral) (Bennie *et al.*, 2014). Factors that influence diel activity patterns may vary between species and include physical characteristics such as the structure of visual systems (Veilleux & Kirk, 2014) to a range of environmental factors including weather conditions (such as temperature) (Herman, 1977; Dussault *et al.*, 2004), predation (Lima & Dill, 1990) and competition avoidance (Carothers & Jaksić, 1984). Although behaviour is generally constrained to the active period, it is important to understand how extrinsic (environmental) variables enhance or constrain the potential for behavioural flexibility and for activity to extend into other phases of the 24-h cycle.

Although diurnal animals typically suppress activity at night, there is increasing evidence that some diurnal animals may increase their activity at night due to factors ranging from migration (Newton, 2008), human avoidance (Graham *et al.*, 2009) and lunar luminosity (Kronfeld-Schor *et al.*, 2013). Among carnivores, increased activity on moonlit nights has been suggested to aid hunting efficiency (Cozzi *et al.*, 2012; Rasmussen & MacDonald, 2012; Broekhuis *et al.*, 2014).

Climatic variables including weather patterns such as wind speed, rain and temperature have the potential to place thermal constraints on animals by altering their core body temperature (Stelzner & Hausfater, 1986; Hill, 2006; Webster *et al.*, 2008). As a response to harsh climatic conditions, endothermic animals (including primates) will alter their behaviour and activity budgets as an attempt to maintain homeothermy (Hill, 2006; Donati *et al.*, 2011; Majolo *et al.*, 2013; Gestich, Caselli & Setz, 2014). Ungulates and rodents living in environments with high summer temperatures will often switch to foraging at night as a means to avoid thermal stress (Herman, 1977;

Dussault *et al.*, 2004; Bourgoin *et al.*, 2011; Hetem *et al.*, 2012). Behavioural plasticity in relation to climatic conditions may be best illustrated in species that live in seasonal environments where fluctuating climatic conditions coupled with limited daylight hours have the potential to alter activity budgets (Dunbar, 1992; Hill *et al.*, 2003a; Hill *et al.*, 2003b; Hill *et al.*, 2004b).

In primates, seasonal shifts in activity have been recorded in cathemeral species, which are found to regularly shift their activity patterns throughout the 24-h diel cycle. Mongoose lemurs (*Eulemur mongoz*) living in seasonally dry forests became more diurnal during the wet season due to lower night-time light intensity and yet became chiefly nocturnal during the dry season when day length was shorter (Curtis, Zaramody & Martin, 1999). In less predictable environments that are characteristic of south-eastern Madagascar, brown collared lemurs (*Eulemur collaris*) shifted their activity levels in response to food availability and thus became more diurnally active when ripe fruit was more readily available (Donati *et al.*, 2007). Despite this remarkable seasonal plasticity, there has been no formal investigation to date of whether such flexibility extends to the use of the nocturnal phase in anthropoids (who are considered strictly diurnal with the exception of *Aotus*) residing in seasonal environments and whether such species can compensate for diurnal time budget constraints, particularly in winter, through nocturnal activity.

In diurnal primates, nocturnal activity in response to increased lunar luminosity has been reported for ring-tailed lemurs (*Lemur catta*) (Parga, 2011; Donati *et al.*, 2013). Chimpanzees (*Pan troglodytes*) have been recorded engaging in behaviours such as feeding (Chivers, 1987), mating (Nishida, 1994) and travelling (Pruetz & Bertolani, 2010) under increased moonlight, although a recent analysis by Tagg *et al.* (2018) found that lunar luminosity had no effect on nocturnal activity in chimpanzees from 22 different populations. Nevertheless, Krief *et al.* (2014) found that chimpanzees in Kibale National Park, Uganda, were more likely to crop raid under moonless nights as a possible means to prevent detection from humans. The interactions between lunar luminosity and nocturnal behaviour in diurnal species are thus not straightforward.

Despite being considered diurnal, baboons have been recorded becoming active at night as a response to lunar luminosity. For example, yellow baboons (*Papio cynocephalus*), in Kenya, had periods of frequent alarm calling with increased nocturnal illumination (Altmann & Altmann, 1970), whereas Guinea baboons (*Papio papio*) in Senegal were found to regularly move throughout the night and to leave sleeping sites earlier in the morning during the dry season when nocturnal illumination was greater (Anderson & McGrew, 1984). Using accelerometers and global positioning system (GPS) collars, Isbell *et al.* (2017) found low levels of nocturnal activity in a group of olive baboons (*Papio anubis*) in Laikipia, Kenya, with movement found to occur on 15% of nights, but there was no clear indication that baboons responded to increased moonlight. Although nocturnal activity may be marginal in equatorial baboons, there has yet to be a formal assessment of nocturnal activity in non-equatorial populations. Such populations are likely to experience significant ecological constraints on time at certain times of year (Hill *et al.*, 2003a; Hill *et al.*, 2003b) such that the adaptive use of the nocturnal phase may allow them to compensate for limits in the diurnal activity period at these times (although decreasing temperatures during winter months may impose thermoregulatory constraints that may lead to a decrease in activity).

Due to practical constraints ranging from inadequate visibility to unintentionally altering natural sleeping habits, previous research on nocturnal activity patterns in diurnal anthropoids has been primarily limited to anecdotal observations (Vessey, 1973; Anderson & McGrew, 1984; Stelzner & Hausfater, 1986; although see Isbell *et al.*, 2017; Tan *et al.*, 2013). However, recent advances in radio telemetry have allowed for the collection of activity data through dual-axis accelerometers attached to GPS collars. Accelerometers have been especially useful in allowing researchers to monitor the behaviour of cryptic species such as pumas (*Puma concolor*) (Williams *et al.*, 2014), badgers (*Meles meles*) (McClune *et al.*, 2014) and lynx (*Lynx lynx)* (Podolski *et al.*, 2013) as well as activity patterns during time periods where behavioural observations are difficult (Cooke *et al.*, 2004; Brown *et al.*, 2013). Accelerometers have also proven effective on primates (including baboons; Markham & Altmann, 2008; Fehlmann *et al.*, 2017; Isbell *et al.*, 2017) and have been employed to assess intragroup (Mann *et al.*, 2005) as well as seasonal variability in activity patterns (Erkert & Kappeler, 2004; Muñoz-Delgado *et al.*, 2005; Eppley, Ganzhorn & Donati, 2015).

Through the aid of accelerometers, we assessed whether temporal and environmental factors, as well as pregnancy, impacted nocturnal activity patterns in chacma baboons (*Papio ursinus*) found in the western Soutpansberg Mountains, Limpopo Province, South Africa. Living in large complex multi-male/multi-female groups, baboons are some of the most widespread primates in Africa (Henzi & Barrett, 2005) inhabiting a variety of different environments that vary significantly in terms of seasonality, food availability and habitat types (Dunbar, 1992). Chacma baboons respond to environmental pressures including seasonal changes in food availability, temperature and day length by not only altering their diet, but also by reallocating their time spent engaging in necessary tasks including resting, feeding and socializing (Dunbar, 1992; Hill *et al.*, 2003b).

Here, we define 'activity' as any movement that is recorded, regardless of the animal's position and behavioural state (Scheibe *et al.*, 1998). Following an assessment that baboons exhibit quantifiable activity levels at night within the Soutpansberg Mountains, South Africa, we then test the following hypotheses:

Hypothesis 1

Baboons will respond to shorter day lengths in winter by extending their activity into the nocturnal phase.

Hypothesis 2

Nocturnal activity will increase on nights exhibiting greater lunar luminosity (i.e. during a full moon) due to increased visual acuity.

Hypothesis 3

Environmental variables will impact nocturnal activity levels due to thermoregulatory constraints. Specifically, activity will decrease as temperature and the wind chill equivalent temperature decreases and wind speed increases, and as precipitation increases.

Materials and methods

Study site

This study was based at the Lajuma Research Centre in the western Soutpansberg Mountains, Limpopo Province, South Africa (23°06′45.14″S 29°11′37.10″E). Having a maximum elevation of 1748 m above sea level (Mostert *et al.*, 2008) and running *c.* 250 km from east to west and 15–60 km from north to south (Berger *et al.*, 2003), the Soutpansberg Mountains are a topographically complex environment consisting of numerous habitats ranging from closed woodlands, mistbelt forests, bushveld complexes, as well as relatively open and rocky sub-alpine mountain bushveld and sourveld ecosystems (Mostert *et al.*, 2008; Kirchhof *et al.*, 2010). The study site has a mean annual rainfall of 724 mm with a summer rainy season (December–February) and a winter dry season (May–August) (Willems, Barton & Hill, 2009). Mean daily minimum and maximum seasonal temperatures throughout the study period ranged from 16.8–17.6°C in winter to 21.2–22.0°C in summer. Mean nightly minimum and maximum temperatures ranged from 12.8 to 13.4°C (winter) and 18.6 to 19.1°C (summer). Day length fluctuates from *c.* 11 h in winter to over 13 h in summer.

Baboon collaring methods and activity data collection

Adult female baboons ($N = 3$) from two groups were fitted with Vectronic GPS-PLUS collars 18 (VECTRONIC Aerospace, Berlin, Germany) between September 2013 and November 2015 (Table 1). One individual was collared twice during the study period, and only females were collared since males periodically transfer between groups.

All baboons were sedated with a combination of 1–1.4 mg kg^{-1} tiletamine/zolazepam (Zoletil; Virbac RSA (Pty) Ltd, Halfway House, South Africa) and 0.02–0.03 mg kg^{-1} medetomidine (Domitor; Pfizer Laboratories (Pty) Ltd, Maywood, NJ, USA), delivered via remote injection dart (DanInject International, Pietermaritzburg, South Africa) before being fitted with a collar. After all procedures were completed, the medetomidine was antagonized with an intramuscular dose of atipamezole (Antisedan; Pfizer Laboratories (Pty)), given at 0.1–0.15 mg kg^{-1}, and the animals were allowed to recover in a crate before being released near to their group.

Collars were programmed to take GPS fixes every hour between 06:00 and 20:00 SAST with one nocturnal fix at 22:00 ($N = 11\,129$; mean fixes per day 15.43 (96.4%). The GPS collars incorporated dual-axis activity sensors which captured acceleration on two axes (*x*-axis and *y*-axis) at 4 Hz, with the data processed and stored as 120s averages. Accelerometers were located at the top of GPS collars and near the back of the animals' neck. Direction of the *x*-axis sensors moved from front to back, whereas the direction of the *y*-axis from side to side as the animals moved. In this case, the *x*-axis represented forward and backward movements and the *y*-axis sideward and rotary movements ('body roll movement') (Berger, Dettki & Urbano, 2014). Our collars did not have accelerometers that incorporate the *z*-axis (up and down movements). Given the strong positive correlation found between the *x*-axis and the *y*-axis (Pearson's $r = 0.953$, $P = <0.0001$), only the *x*-axis data were used in analysis (following Heurich *et al.*, 2014). Activity values derived from sensors range from 0 (no activity) to 255 (high activity).

Most GPS collars fell off when designated (378 days after the collars were fitted) with the exception of one collar which fell off earlier than expected. All data were downloaded regularly through an ultra high frequency terminal.

Predictor variables

Data from between 20 min after the onset and 20 min before the conclusion of astronomical twilight were extracted for analysis in order to completely ensure that only nocturnal data were included (Bearder, Nekaris & Curtis, 2006) (night-time hours in these analyses range from 13 h in winter and 10.45 h in summer, $N = 777$). Astronomical twilight defines a time range when the sun (disc) is 18° below the horizon such that the data selection ensured that baboons could not see without additional illumination. Times for the onset and conclusion of astronomical twilight across the duration to this study derived from the National Aeronautics and Space Administration (NASA) database (https://www.usno.navy.mil/).

Local climatic data including rain, temperature, wind speed and wind chill equivalent temperature were collected from an on-site South African Environmental Observation Network (SAEON) weather station. The wind chill equivalent temperature combines temperature and wind speed to estimate the perceived environmental temperature (Hill *et al.*, 2004a). Precipitation was measured as the rainfall in a half-hour interval or the average nightly rainfall depending on the analysis (see Statistical analysis).

Table 1 Global positioning system collared baboon information

Collar ID	Date collared from	Data collected until	Sex	Group	Notes
11941	09/03/2013	05/02/2014	F	Habituated	–
11940	11/06/2015	14/08/2015	F	Unhabituated	–
11942	27/07/2014	30/05/2015	F	Habituated	Gave birth to infant in March 2015
11938	04/06/2015	18/7/2015	F	Habituated	Same individual as Collar ID 11942

Lunar luminosity, defined as the percentage of the lunar sphere that is visible due to illumination by the sun, was used to assess whether moonlight influenced baboon nocturnal activity. Lunar luminosity, daily moonrise and set times, and day length (being the period in which the Earth receives illumination from the sun) were downloaded from NASA's data services (https://data.nasa.gov/) and synchronized to the data set. Lunar luminosity was continuous with values ranging between 0% (moon not visible) and 100% (fully visible). Since lunar luminosity is constrained to times in which the moon is visible in the night sky (above the horizon), lunar luminosity values were constrained by moonrise and set times each night. Unfortunately, cloud coverage data could not be obtained for these analyses.

Statistical analysis

In order to test the three hypotheses, nocturnal activity data were separated into two different datasets. Data set A consisted of average activity throughout each night within the study period ($N = 777$) and allowed a broad-scale analysis (Model A) for an overall assessment of seasonal trends. Data set B ($N = 14\,019$) comprised of average activity in half-hour intervals (i.e. the average activity within every half-hour for each individual night). Data set B permitted a fine-scaled model (Model B) with the inclusion of environmental variables that may shift throughout the night.

Generalized linear mixed models (GLMM) with a gamma error structure and log-link function (Bates *et al.*, 2015) were used to assess total activity levels (both broad scale (Model A) and fine scale (Model B) across nights in RStudio (Version 0.98.1103; RStudio, Inc., Boston, MA, USA). A gamma error structure was selected for all GLMMs given the continuous and positive structure of the data as well as the near-constant variance found on the log scale. Log-link functions are generally used with gamma error structures. Activity data were transformed by adding 1 to all values to fulfil the requirements for a gamma GLMM.

Day length was included in both coarse and fine-grained models to assess whether baboons responded to shorter days by extending their nocturnal activity levels throughout the night (H1). To assess the impact that the lunar cycle had on baboon activity levels (H2), lunar luminosity was included in the coarse-grained model (Model A), with the luminescence value corrected for the presence of the moon combined in Model B (fine-grained model). Mean nightly wind chill temperatures and precipitation levels were included in Model A to assess the impact of weather variables (H3). We used mean instead of lowest temperature for Model A since the meteorological data allowed us to account for the variability in temperatures across each half-hour interval rather than using a single coldest value for the night. Temperature, wind speed (and the interaction between the two) and rainfall levels at half-hour intervals were included to assess whether fluctuating environmental variables had a fine-grained influence on baboon nocturnal activity levels (Model B).

To account for intergroup, individual and nightly variability, collar identity ($N = 4$) specific groups ($N = 2$), night ($N = 777$) and sleeping site identity (derived from the nocturnal GPS fix and ground-truthed with observational data, $N = 19$) were included as random effects. Collar identity was preferred as a random effect over individual identity due to possible differences in collar performance. As one collared female gave birth during data collection, the presence of an infant was thus included as a factor to account for the costs of maternal care such as infant carrying, suckling and increased vigilance (Altmann & Samuels, 1992; Rendall, Cheney & Seyfarth, 2000; Maestripieri, 2011) impacting on nocturnal activity. Subsequent results were analysed in RStudio and visualized with the aid of the ggplot2 package (Wickham, 2009).

Results

Although nocturnal activity levels were far below those observed during the day, consistent, but low levels of activity were observed during the nocturnal phase [diurnal defined as the hours after sunrise and before sunset ($N = 777$, $\bar{x} = 64.57$, SE = 0.379) and nocturnal as the hours after sunset and before sunrise ($N = 777$, $\bar{x} = 1.76$, SE = 0.029)]. During the twilight phases, when the sun still has an impact on the illumination available, activity was 16% of that observed during the diurnal period ($N = 765$, $\bar{x} = 10.65$, SE = 0.285; Fig. 1).

Model A included lunar luminosity, wind chill equivalent temperature, precipitation and day length as predictor variables (Table 2) and represented a significant improvement over the null model (the control variables, presence of an infant, day length and random effects (likelihood ratio test: $x^2 = 80.42$, d.f. = 4, $P < 0.0001$). In support of Hypothesis 1, a significant negative relationship between day length and nocturnal activity levels suggests that baboons increase nocturnal activity as day length declines. In support of Hypothesis 2, there was a significant positive relationship between baboon activity levels and lunar luminosity with baboons more active on nights with greater light intensity. There was no support for Hypothesis 3 that perceived temperature (through wind chill) or higher levels of nightly precipitation impacted baboon activity patterns throughout the night. Nocturnal activity significantly decreased with the presence of a dependent infant.

Model B assessed a fine-scale analysis of activity throughout the night and included combined moon presence and lunar luminosity as well as temperature and wind speed and their interaction (Table 3). Overall, the full model was highly significant compared with the null model (including random effects, day length and presence of an infant; $x^2 = 17.52$, d.f. = 5, $P = 0.003$). In support of Hypothesis 2, lunar light intensity had a significant positive effect on baboon nocturnal activity levels, with activity increasing with higher nocturnal illumination. There was no support for wind speed or precipitation impacting nocturnal activity levels nor the interaction between temperature and wind speed (Hypothesis 3). Contrary to expectations, there was a significant negative relationship between temperature and activity levels, with activity increasing when night-time temperatures were coldest. The reduction in activity levels in the presence of an infant remained significant, as was the relationship with day length (Hypothesis 1).

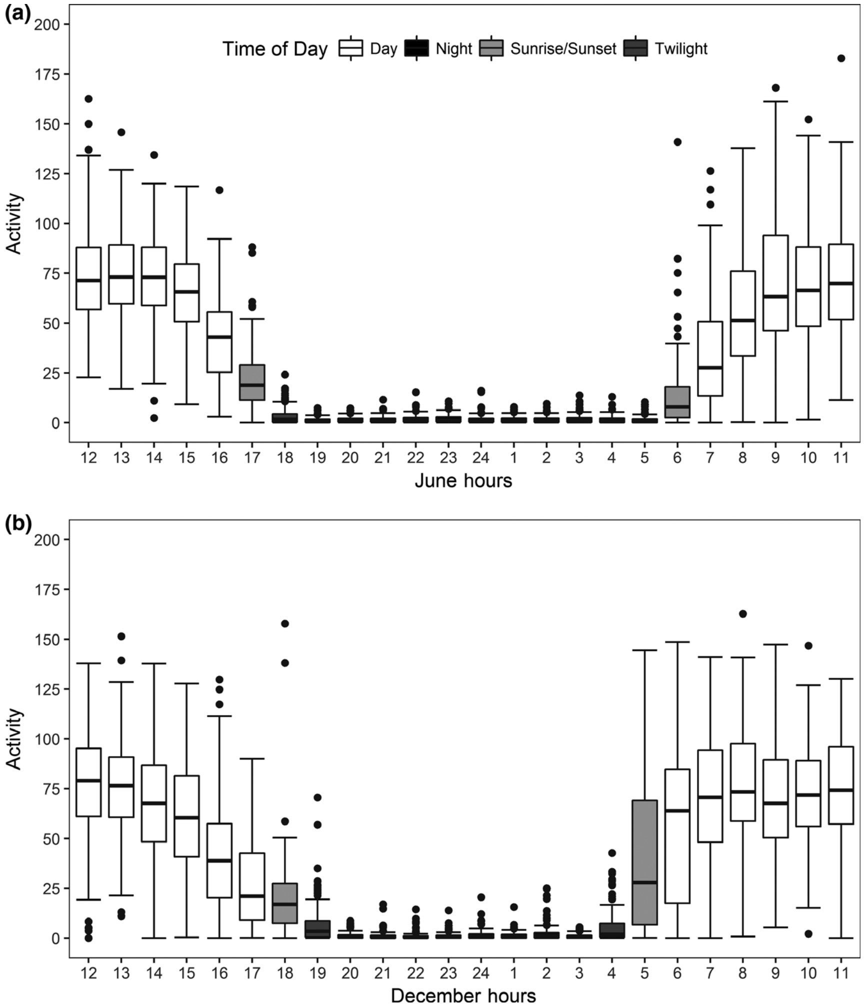

Figure 1 Boxplots (median, lower and upper quartiles, and one standard error) of activity levels of chacma baboons across the 24-hr cycle under conditions of (a) minimum day length/maximum night length in winter (June; mean day length: 10h 44m) and (b) maximum day length/minimum night length in summer (December; mean day length: 13 h 31 min). Twilight hours for (a) (winter) are 5:00 and 18:00. Twilight hours for (b). (summer) are 4:00 and 19:00. Activity levels range from 0 (low activity) to a maximum of 255 (high activity).

Table 2 Coefficients for coarse-grained analysis of seasonal nocturnal activity (Model A; random effects include individual, night, sleeping site and baboon group)

Fixed effects	Estimate	SE	*t* value	Pr(>|*z*|)
Intercept	2.0286	0.1665	12.179	**<0.0001**
Lunar luminosity	0.0741	0.0259	2.859	**0.0042**
Wind chill	−0.0010	0.0024	−0.421	0.6734
Precipitation	0.0526	0.0407	1.292	0.1964
Day length	−2.2643	0.3176	−7.129	**<0.0001**
Infant presence	−0.3312	0.0399	−8.288	**<0.0001**

Significant coefficents are highlighted in bold.

Discussion

A coarse-grained model (Model A) indicated that varying daylight hours and levels of lunar light intensity may alter nocturnal activity in baboons ($N = 3$) in the western Soutpansberg Mountains. In addition, a fine-scale analysis demonstrated that temperature, the presence of the moon (coupled with lunar light intensity) and day length impacted baboon activity levels throughout the course of the night. For both analyses, the presence of an infant had a significant negative effect on the nocturnal activity levels of the adult female. Collectively, these analyses appear to support two out of the three hypotheses (H1 and H2), with baboons seeming to respond to environmental conditions through changes in nocturnal behaviour. However, the fact that levels of nocturnal activity are very low throughout the year suggests that such patterns could simply reflect intermittent sleep disturbances rather than specific activity by the baboons.

In support of Hypothesis 1, baboons increased their nocturnal activity levels in response to shorter day lengths in winter. As previous studies have described the importance of day length in constraining the activity budgets of diurnal primates

Table 3 Coefficients for fine-grained analysis of trends in activity throughout the night (Model B; random effects include individual, night, sleeping site and baboon group)

Fixed effects	Estimate	SE	*t* value	Pr(>|*z*|)
Intercept	2.3390	0.1662	14.071	**<0.0001**
Lunar luminosity	0.0483	0.0210	2.297	**0.0216**
Temperature	−0.0079	0.0029	−2.661	**0.0077**
Wind speed	−0.0042	0.0050	−0.843	0.3992
Precipitation	−0.0084	0.0163	−0.516	0.6061
Temperature: wind speed interaction	0.0005	0.0003	1.574	0.1154
Day length	−2.4552	0.3468	−7.079	**<0.0001**
Infant presence	−0.3021	0.0369	−8.168	**<0.0001**

Significant coefficents are highlighted in bold.

living in seasonal environments (Hill *et al.*, 2003b; Ménard *et al.*, 2013), it is possible that baboons may engage in activities such as social behaviour that may otherwise be severely constrained by shorter day lengths and increased diurnal foraging in winter. Our data are not at a resolution to allow us to explore this formally, but given the low nocturnal activity in general it is more likely that activity increases are simply due to longer nights during winter exceeding the time needed for sleep. As such, although baboons exhibited higher activity levels during these periods, this could simply reflect the fact that the animals are awake and shifting position slightly rather than exhibiting heightened activity after dark.

If baboons are not compensating for short day lengths with increased activity at night, one expectation might be that the animals should start moving sooner in winter as soon as light becomes available. Interestingly, our results suggest that the baboons became active earlier in summer (Fig. 1), complementing previous studies showing that primates wake up earlier in summer (Erkert & Kappeler, 2004; Urbanski, 2011). This could be a strategy to be active earlier to avoid higher midday temperatures (Huang *et al.*, 2003; Hill, 2006; Zhou *et al.*, 2007; Aublet *et al.*, 2009; Paulo & Lopes, 2014), although it is important to note that earlier summer activity may not be associated with an earlier departure from the sleeping site. Unfortunately, our GPS data are not at a sufficient resolution to determine the timing of departure in relation to sunrise. Hall (1962) found that the baboons at Cape Point, South Africa, began their active day earlier during the winter months, although subsequently concluded that emergence times were independent of sunrise. However, Davidge (1978) reported that the baboons rested longer immediately following emergence from their sleeping site during the winter months, possibly as a response to a need to warm up in direct sunshine (see Stelzner & Hausfater, 1986). Thermoregulatory considerations may thus mask any movement response to the constraints of short days and long nights in winter.

Lunar luminosity had a positive effect on nocturnal activity levels in both models, supporting Hypothesis 2. Baboons were more active on nights exhibiting greater lunar light intensity, but only at times when the moon was visible above the horizon. Baboons did not travel or forage with increased lunar luminosity and remained on their relatively narrow sleeping cliffs at night. Although baboons in the western Soutpansberg Mountains have been recorded being predated on by leopards (*Panthera pardus*) on their sleeping sites at night, it seems likely that lunar luminosity may inhibit leopards from attacking. This is primarily because ambush predators (such as felids) are generally less successful at hunting at such times due a reduction in ambush cover that would otherwise be provided on darker nights (Sunquist & Sunquist, 1989; Martins & Harris, 2013). Nevertheless, Bidner, Matsumoto-Oda & Isbell, (2018) found that lunar luminosity did not influence leopard visitation rates at sleeping sites in Laikipia, Kenya, suggesting that some elements of predator behaviour are not influenced by the lunar cycle.

While many nocturnal and cathemeral primates exhibit higher activity levels on full moons (Gursky, 2003; Kronfeld-Schor *et al.*, 2013), it seems likely that for many species, nights exhibiting greater light intensity may simply have a stimulating effect that supersedes standard circadian activity patterns (i.e. positive masking) (Donati *et al.*, 2013). Such an effect may be especially true in primate species such as chacma baboons that lack a specialized visual structure that aids in nocturnal vision (the *tapetum lucidum*).

Although our data do not show significant movement away from the sleeping site between 20:00 and 22:00 (median 10.24 m, range: 0.00–773.26 m, GPS accuracy = 5 m or less, $N = 623$), baboons in western Soutpansberg exhibited seemingly greater nocturnal activity patterns compared with those in equatorial Kenya (Isbell *et al.*, 2017). Nevertheless, there were several nights where baboons moved greater distances (>100 m; $N = 57$) with anecdotal observations, particularly alarm vocalisations, suggesting they may have been driven from their sleeping sites by the presence of a predator (unpublished data). Even so, there was no correlation between distance moved and activity levels in those 2 h ($r = -0.05$, $N = 605$, $P = 0.218$), suggesting that this cannot account for our results. Despite occasionally moving large distances, therefore, the generally low activity levels at night appear to simply reflect disturbed sleep patterns.

A number of factors have been found to reduce sleep quality in non-human primates, including weather conditions (such as wind and rain) and disturbance by either predators or members of their own group (Anderson, 2000). Our results suggest that lunar luminosity may possibly cause sleep disturbances in baboons and altered sleep patterns due to environmental conditions (Navara & Nelson, 2007) and increased nocturnal light exposure in urban environments have been found in humans

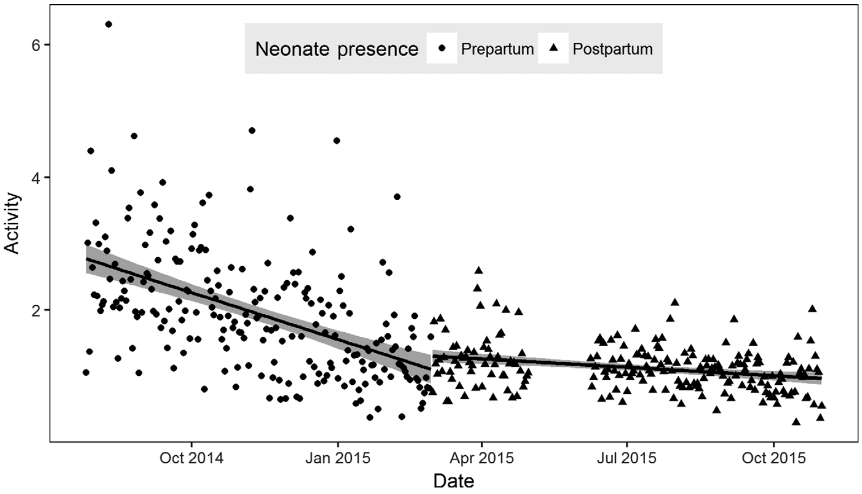

Figure 2 Relationship between nightly nocturnal activity levels and the presence of an infant in chacma baboons (one activity value per night).

(Munezawa *et al.*, 2011; Ohayon & Milesi, 2016). Interestingly, melatonin (a hormone that regulates sleep and wake patterns) suppression in humans can be achieved after being exposed to 90 min of light levels equivalent to a full moon (Brainard *et al.*, 2001) leading to a loss in quality of sleep. Baboons sleeping on cliffs, therefore, may experience similar issues with lower sleep quality on moonlit nights.

Female baboons in the western Soutpansberg increased their activity on nights with cooler temperatures, contrary to our predictions for Hypothesis 3. Baboons, like other primates and mammals, are known to respond to thermoregulatory constraints by huddling with one another (Gilbert *et al.*, 2010). While such a strategy allows for heat conservation and leads to the prediction that activity should decline at low temperatures, previous research on Guinea baboons suggests that individuals may often alter their positions throughout the night as a response to changing climatic conditions (such as wind speed and rain) (Anderson & McGrew, 1984). The significant effect of temperature on baboon activity in the western Soutpansberg may thus simply reflect localized conditions and sleeping site preference and a response to colder conditions by changing huddling positions throughout the night. Although Anderson & McGrew (1984) did not find temperature to have an effect on postural adjustments, it should be noted that the relatively warmer conditions that are characteristic of Niokolo Koba National Park, Senegal, may negate the need for such behaviours.

An interesting outcome of our analyses was that nocturnal activity levels for one female dropped significantly after giving birth (Fig. 2). While this might be in contrast to predictions that infant presence may increase activity, it should be recognized that with the exception of one non-human primate study (Fite *et al.*, 2003), such expectations were driven primarily from research involving maternal sleep disturbances in human mothers (Nishihara & Horiuchi, 1998; Dennis & Ross, 2005; Goyal, Gay & Lee, 2007). In the context of baboons, there have been several studies highlighting the costly demands associated with infant rearing (Dunbar & Dunbar, 1988; Altmann & Samuels, 1992). Interestingly, Barrett *et al.* (2006) found that baboons at De Hoop Nature Reserve (South Africa) did not increase time spent feeding as a response to infant rearing but instead suppressed their diurnal activity levels by resting more frequently during the day (possibly due to general fatigue after giving birth). The results here suggest that females with infants may also increase resting and inactivity at night, although it is important to note that the activity sensors we used were not able to pick up subtle behaviours associated with infant suckling. Nevertheless, the fact that nocturnal activity also declines across pregnancy suggests that there are energetic consequences of pregnancy and infant rearing that are reflected in increased resting requirements at night.

Despite having been effective in the assessment of primate movement (Papailiou, Sullivan & Cameron, 2008; McFarland *et al.*, 2013), the data derived from accelerometers in this analysis can only be utilized to assess how overall trends in nocturnal activity are impacted by a specific attribute. Since the GPS collars attached to the baboons only collected a single fix late at night, it was not possible to supplement this information with additional behavioural data. While the rise in nocturnal activity after shorter days and on moonlit nights probably points to baboons making small adjustments, additional data are needed to assess whether baboons reallocate specific behaviours to the nocturnal period. Infrared cameras have successfully been utilized to assess nocturnal behaviours in diurnal species (Barrett *et al.*, 2004; Gula *et al.*, 2010; Thuppil & Coss, 2016) and may therefore be valuable for remotely determining temporal trends in nocturnal activity. In addition, fine-scale GPS data in conjunction with accelerometers should also permit more refined analysis (Fehlmann *et al.*, 2017). Finally, we suggest that future research should ideally use accelerometers that incorporate the *z*-axis (up and down movements) when assessing the movement patterns of terrestrial mammals. This would not only allow for a more refined assessment of movement patterns, but may also allow the identification of specific behaviours (Shepard *et al.*, 2010).

Results from two generalized linear mixed models show that shorter days, increased lunar luminosity and lower temperatures had a weak (but positive) effect on nocturnal activity levels in chacma baboons. Given that the effect sizes of the relationships were modest, it seems likely that sleep was simply more interrupted under conditions of long winter nights, high lunar illumination and at cold temperatures. Future research should focus on identifying the precise behaviours exhibited during heightened activity in the nocturnal phase to better understand how diurnal primates living in temperature latitudes respond to fluctuating environmental conditions.

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References

Altmann, S.A. & Altmann, J. (1970). *Baboon ecology: African field research*. Chicago, IL: University of Chicago Press.

Altmann, J. & Samuels, A. (1992). Costs of maternal care: infant-carrying in baboons. *Behav. Ecol. Sociobiol.* **29**, 391–398.

Anderson, J.R. (2000). Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Med. Rev.* **4**, 355–373.

Anderson, J.R. & McGrew, W.C. (1984). Guinea baboons (Papio papio) at a sleeping site. *Am. J. Primatol.* **6**, 1–14.

Aublet, J.F., Festa-Bianchet, M., Bergero, D. & Bassano, B. (2009). Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia* **159**, 237–247.

Barrett, L., Gaynor, D., Rendall, D., Mitchell, D. & Henzi, S.P. (2004). Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *J. Hum. Evol.* **46**, 215–222.

Barrett, L., Halliday, J. & Henzi, S.P. (2006). The ecology of motherhood: the structuring of lactation costs by chacma baboons. *J. Anim. Ecol.* **75**, 875–886.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 51.

Bearder, S.K., Nekaris, K.A.I. & Curtis, D.J. (2006). A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatol.* **77**, 50–71.

Bennie, J.J., Duffy, J.P., Inger, R. & Gaston, K.J. (2014). Biogeography of time partitioning in mammals. *Proc. Natl. Acad. Sci. USA* **111**, 13727–13732.

Berger, L.R., De Ruiter, D.J., Steininger, C.M. & Hancox, J. (2003). Preliminary results of excavations at the newly investigated Coopers D deposit, Gauteng, South Africa. *S. Afr. J. Sci.* **99**, 276–278.

Berger, A., Dettki, H. & Urbano, F. (2014).Deciphering animals' behaviour: joining GPS and activity data. In *Spatial database for GPS wildlife tracking data*: 231–244. Urbano, F. & Cagnacci, F. (Eds). New York, NY: Springer.

Bidner, L.R., Matsumoto-Oda, A. & Isbell, L.A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *Am. J. Primatol.* **80**, e22932.

Bourgoin, G., Garel, M., Blanchard, P., Dubray, D., Maillard, D. & Gaillard, J.-M. (2011). Daily responses of mouflon (Ovis gmelini musimon × Ovis sp.) activity to summer climatic conditions. *Can. J. Zool.* **89**, 765–773.

Brainard, G.C., Hanifin, J.P., Greeson, J.M., Byrne, B., Glickman, G., Gerner, E. & Rollag, M.D. (2001). Action spectrum for melatonin regulation in humans: evidence for a novel circadian photoreceptor. *J. Neurosci.* **16**, 6405–6412.

Broekhuis, F., Grünewälder, S., McNutt, J.W. & Macdonald, D.W. (2014). Optimal hunting conditions drive circalunar behavior of a diurnal carnivore. *Behav. Ecol.* **25**, 1268–1275.

Brown, D.D., Kays, R., Wikelski, M., Wilson, R. & Klimley, A.P. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelemetry* **1**, 20.

Carothers, J.H. & Jaksic, F.M. (1984). Time as a niche difference: the role of interference competition. *Oikos* **42**, 403–406.

Chivers, D.J. (1987). The chimpanzees of Gombe: patterns of behavior. *J. Trop. Ecol.* **2**, 327–347.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* **19**, 334–343.

Cozzi, G., Broekhuis, F., McNutt, J.W., Turnbull, L.A., Macdonald, D.W. & Schmid, B. (2012). Fear of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa ' s large carnivores Fear of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa ' s large carnivores. *Ecology* **93**, 2590–2599.

Curtis, D.J., Zaramody, A. & Martin, R.D. (1999). Cathemerality in the mongoose lemur, *Eulemur mongoz*. *Am. J. Primatol.* **47**, 279–298.

Davidge, C. (1978). Activity patterns of Chacma Baboons (*Papio ursinus*) at Cape Point. *Zool. Africana* **13**, 143–155.

Dennis, C.-L. & Ross, L. (2005). Relationships among infant sleep patterns, maternal fatigue, and development of depressive symptomatology. *Birth* **32**, 187–193.

Donati, G., Bollen, A., Borgognini-Tarli, S.M. & Ganzhorn, J.U. (2007). Feeding over the 24-h cycle: Dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). *Behav. Ecol. Sociobiol.* **61**, 1237–1251.

Donati, G., Ricci, E., Baldi, N., Morelli, V. & Borgognini-Tarli, S.M. (2011). Behavioral thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic and dietary-related factors. *Am. J. Phys. Anthropol.* **144**, 355–364.

Donati, G., Santini, L., Razafindramanana, J., Boitani, L. & Borgognini-Tarli, S. (2013). (Un-)expected nocturnal activity in “diurnal” *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. *Am. J. Phys. Anthropol.* **150**, 99–106.

Dunbar, R.I.M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.* **31**, 35–49.

Dunbar, R.I.M. & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Anim. Behav.* **36**, 970–980.

Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L. & Larochelle, J. (2004). Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* **11**, 321–328.

Eppley, T.M., Ganzhorn, J.U. & Donati, G. (2015). Cathemerality in a small, folivorous primate: proximate control of diel activity in Hapalemur meridionalis. *Behav. Ecol. Sociobiol.* **69**, 991–1002.

Erkert, H.G. & Kappeler, P.M. (2004). Arrived in the light: Diel and seasonal activity patterns in wild Verreaux’s sifakas (Propithecus v. verreauxi; Primates: Indriidae). *Behav. Ecol. Sociobiol.* **57**, 174–186.

Fehlmann, G., O’Riain, M.J., Hopkins, P.W., O’Sullivan, J., Holton, M.D., Shepard, E.L.C. & King, A.J. (2017). Identification of behaviours from accelerometer data in a wild social primate. *Anim. Biotelemetry* **5**, 6.

Fite, J.E., French, J.A., Patera, K.J., Hopkins, E.C., Rukstalis, M., Jensen, H.A. & Ross, C.N. (2003). Nighttime wakefulness associated with infant rearing in Callithrix kuhlii. *Int. J. Primatol.* **24**, 1267–1280.

Gestich, C.C., Caselli, C.B. & Setz, E.Z.F. (2014). Behavioural thermoregulation in a small neotropical primate. *Ethology* **120**, 331–339.

Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J.M., Giroud, S., Blanc, S. & Ancel, A. (2010). One for all and all for one: the energetic benefits of huddling in endotherms. *Biol. Rev.* **85**, 545–569.

Goyal, D., Gay, C.L. & Lee, K.A. (2007). Patterns of sleep disruption and depressive symptoms in new mothers. *J. Perinat. Neonatal Nurs.* **21**, 123–129.

Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* **12**, 445–455.

Gula, R., Theuerkauf, J., Rouys, S. & Legault, A. (2010). An audio/video surveillance system for wildlife. *Eur. J. Wildl. Res.* **56**, 803–807.

Gursky, S. (2003). Lunar philia in a nocturnal primate. *Int. J. Primatol.* **24**, 351–367.

Hall, K.R.L. (1962). Numerical data, maintenance activities and locomotion of the wild chacma baboon, *Papio ursinus*. *Proc. Zool. Soc. London* **139**, 181–220.

Henzi, S.P. & Barrett, L. (2005). The historical socioecology of savanna baboons (Papio hamadryas). *J. Zool.* **265**, 215–226.

Herman, T.B. (1977). Activity patterns and movements of subarctic voles. *Oikos* **29**, 434–444.

Hetem, R.S., Strauss, W.M., Fick, L.G., Maloney, S.K., Meyer, L.C.R., Shobrak, M., Fuller, A. & Mitchell, D. (2012). Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology* **115**, 411–416.

Heurich, M., Hilger, A., Küchenhoff, H., Andrén, H., Bufka, L., Krofel, M., Mattisson, J., Odden, J., Persson, J., Rauset, G.R., Schmidt, K. & Linnell, J.D.C. (2014). Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. *PLoS ONE* **9**, e114143.

Hill, R.A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *Am. J. Phys. Anthropol.* **129**, 242–249.

Hill, R.A., Barrett, L., Gaynor, D., Weingrill, A., Dixson, P., Payne, H.F.P. & Henzi, S.P. (2003a). Day length, latitude and behavioural (in)flexibility in Baboons (*Papio cynocephalus ursinus*). *Behav. Ecol. Sociobiol.* **53**, 278–286.

Hill, R.A., Barrett, L., Gaynor, D., Weingrill, T., Dixon, P., Payne, H. & Henzi, S.P. (2003b). Day length, latitude and behavioural (in) flexibility in baboons (*Papio cynocephalus ursinus*). *Behav. Ecol. Sociobiol.* **53**, 278–286.

Hill, R.A., Barrett, L., Gaynor, D., Weingrill, T., Dixon, P., Payne, H. & Henzi, S.P. (2004a). Day length variation and seasonal analysis of behaviour. *South African J. Wildl. Res.* **34**, 39–44.

Hill, R.A., Weingrill, T., Barrett, L. & Henzi, S.P. (2004b). Indices of environmental temperatures for primates in open habitats. *Primates* **45**, 7–13.

Huang, C., Wei, F., Li, M., Li, Y. & Sun, R. (2003). Sleeping cave selection, activity pattern and time budget of white-headed langurs. *Int. J. Primatol.* **24**, 813–824.

Isbell, L.A., Bidner, L.R., Crofoot, M.C., Matsumoto-Oda, A. & Farine, D.R. (2017). GPS-identified, low-level nocturnal activity of vervets (Chlorocebus pygerythrus) and olive baboons (Papio anubis) in Laikipia, Kenya. *Am. J. Phys. Anthropol.* **164**, 203–211.

Kirchhof, S., Krämer, M., Linden, J. & Richter, K. (2010). The reptile species assemblage of the Soutpansberg (Limpopo Province, South Africa) and its characteristics. *Salamandra* **46**, 147–166.

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.M. & Masi, S. (2014). Wild chimpanzees on the edge: Nocturnal activities in croplands. *PLoS ONE* **9**, e109925.

Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E.D., Dayan, T. & Helfrich-Forster, C. (2013). Chronobiology by moonlight. *Proc. R. Soc. B Biol. Sci.* **280**. 20123088.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.

Maestripieri, D. (2011). Emotions, stress, and maternal motivation in primates. *Am. J. Primatol.* **73**, 516–529.

Majolo, B., McFarland, R., Young, C. & Qarro, M. (2013). The effect of climatic factors on the activity budgets of Barbary Macaques (Macaca sylvanus). *Int. J. Primatol.* **34**, 500–514.

Mann, T.M., Williams, K.E., Pearce, P.C. & Scott, E.A.M. (2005). A novel method for activity monitoring in small non-human primates. *Lab. Anim.* **39**, 169–177.

Markham, A.C. & Altmann, J. (2008). Remote monitoring of primates using automated GPS technology in open habitats. *Am. J. Primatol.* **70**, 495–499.

Martins, Q. & Harris, S. (2013). Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *Afr. J. Ecol.* **51**, 571–579.

McClune, D.W., Marks, N.J., Wilson, R.P., Houghton, J.D., Montgomery, I.W., McGowan, N.E., Gormley, E. & Scantlebury, M. (2014). Tri-axial accelerometers quantify behaviour in the Eurasian badger (*Meles meles*): towards an automated interpretation of field data. *Anim. Biotelemetry* **2**, 5.

McFarland, R., Hetem, R.S., Fuller, A., Mitchell, D., Henzi, S.P. & Barrett, L. (2013). Assessing the reliability of biologger techniques to measure activity in a free-ranging primate. *Anim. Behav.* **85**, 861–866.

Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., Vallet, D., Qarro, M. & Pierre, J.S. (2013). Effect of habitat quality on the ecological behaviour of a temperate-living primate: time-budget adjustments. *Primates* **54**, 217–228.

Mostert, T.H.C., Bredenkamp, G.J., Klopper, H.L., Verwe, C., Mostert, R.E. & Hahn, N. (2008). Major vegetation types of the Soutpansberg conservancy and the blouberg nature reserve, South Africa. *Koedoe* **50**, 32–48.

Munezawa, T., Kaneita, Y., Osaki, Y., Kanda, H., Minowa, M., Suzuki, K., Higuchi, S., Mori, J., Yamamoto, R. & Ohida, T. (2011). The association between use of mobile phones after lights out and sleep disturbances among Japanese adolescents: a nationwide cross-sectional survey. *Sleep* **8**, 1013–1020.

Muñoz-Delgado, J., Fuentes-Pardo, B., Euler Baum, A., Lanzagorta, N., Arenas-Rosas, R., Santillán-Doherty, A.M., Guevara, M.A. & Corsi-Cabrera, M. (2005). Presence of a circadian rhythm in the spider Monkey's (Ateles geoffroyi) motor activity. *Biol. Rhythm Res.* **36**, 115–122.

Navara, K.J. & Nelson, R.J. (2007). The dark side of light at night: Physiological, epidemiological, and ecological consequences. *J. Pineal Res.* **43**, 215–224.

Newton, I. (2008). *The ecology of bird migration*. London: Academic Press.

Nishida, T. (1994). Review of recent findings on mahale chimpanzees implications. In *Chimpanzee cultures*: 373–396. Wrangham, R.W., McGrew, W.C., de Waal, F.B.M. & Heltne, P.G. (Eds). Cambridge, MA: Harvard Univ. Press.

Nishihara, K. & Horiuchi, S. (1998). Changes in sleep patterns of young women from late pregnancy to postpartum: relationships to their infants' movements. *Percept. Mot. Skills* **87**, 1043–1056.

Ohayon, M.M. & Milesi, C. (2016). Artificial outdoor nighttime lights associate with altered sleep behavior in the American general population. *Sleep* **39**, 1311–1320.

Papailiou, A., Sullivan, E. & Cameron, J.L. (2008). Behaviors in rhesus monkeys (Macaca mulatta) associated with activity counts measured by accelerometer. *Am. J. Primatol.* **70**, 185–190.

Parga, J.A. (2011). Nocturnal ranging by a diurnal primate: Are ring-tailed lemurs (*Lemur catta*) cathemeral? *Primates* **52**, 201–205.

Paulo, J.L. & Lopes, F.A. (2014). Daily activity patterns of Saanen goats in the semi-arid northeast of Brazil. *Rev. Bras. Zootec* **43**, 464–470.

Podolski, I., Belotti, E., Bufka, L., Reulen, H. & Heurich, M. (2013). Seasonal and daily activity patterns of free-living Eurasian lynx Lynx lynx in relation to availability of kills. *Wildlife Biol.* **19**, 69–77.

Pruetz, J. & Bertolani, P. (2010). Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savannah-mosaic environment: implications for hominin adaptations to open habitats. *PaleoAnthropology* **252**, 262.

Rasmussen, G.S.A. & MacDonald, D.W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *J. Zool.* **286**, 232–242.

Rendall, D., Cheney, D.L. & Seyfarth, R.M. (2000). Proximate factors mediating "contact" calls in adult female baboons (*Papio cynocephalus ursinus*) and their infants. *J. Comp. Psychol.* **114**, 36–46.

Scheibe, K.M., Schleusner, T., Berger, A., Eichhorn, K., Langbein, J., Dal Zotto, L. & Streich, W.J. (1998). ETHOSYS (R) - New system for recording and analysis of behaviour of free-ranging domestic animals and wildlife. *Appl. Anim. Behav. Sci.* **55**, 195–211.

Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Halsey, L.G., Gleiss, A., Morgan, D.T., Myers, A.E., Newman, C. & Macdonald, D.W. (2010). Identification of animal movement patterns using tri-axial accelerometry. *Endanger. Species Res.* **10**, 47–60.

Stelzner, J.K. & Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow baboons. *Primates* **27**, 449–463.

Sunquist, M.E. & Sunquist, F.C. (1989). Ecological constraints on predation by large felids. In *Carnivore behavior, ecology, and evolution*: 283–301.Gittleman, J.L. (Ed). Ithaca, NY: Cornell University Press.

Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., Stewart, F., *et al*. (2018). Nocturnal activity in wild chimpanzees (*Pan troglodytes*): Evidence for flexible sleeping patterns and insights into human evolution. *Am. J. Phys. Anthropol.* **166**, 510–529.

Tan, C.L., Yang, Y. & Niu, K. (2013). Into the night: Camera traps reveal nocturnal activity in a presumptive diurnal primate, Rhinopithecus brelichi. *Primates* **54**, 1–6.

Thuppil, V. & Coss, R.G. (2016). Playback of felid growls mitigates crop-raiding by elephants Elephas maximus in southern India. *Oryx* **50**, 329–335.

Urbanski, H.F. (2011). Circadian variation in the physiology and behavior of humans and nonhuman primates. In *Neuromethods*: 217–235. Raber, J. (Ed). New York, NY: Humana Press.

Veilleux, C.C. & Kirk, E.C. (2014). Visual acuity in mammals: Effects of eye size and ecology. *Brain. Behav. Evol.* **83**, 43–53.

Vessey, S.H. (1973). Night observations of free-ranging rhesus monkeys. *Am. J. Phys. Anthropol.* **38**, 613–619.

Webster, J.R., Stewart, M., Rogers, A.R. & Verkerk, G.A. (2008). Assessment of welfare from physiological and behavioural responses of New Zealand dairy cows exposed to cold and wet conditions. *Anim. Welf.* **17**, 19–26.

Wickham, H. (2009). ggplot2 elegant graphics for data analysis. New York, NY: Springer Publishing Company.

Willems, E.P., Barton, R.A. & Hill, R.A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behav. Ecol.* **20**, 985–992.

Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H. & Wilmers, C.C. (2014). Instantaneous energetics of cougar kills reveals advantage of felid sneak attacks. *Science* **346**, 81–85.

Zhou, Q., Wei, F., Huang, C., Li, M., Ren, B. & Luo, B. (2007). Seasonal variation in the activity patterns and time budgets of Trachypithecus francoisi in the Nonggang Nature Reserve, China. *Int. J. Primatol.* **28**, 657–671.

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REVIEW ARTICLE

Anthropogenic influences on primate antipredator behavior and implications for research and conservation

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Abstract

Predation risk affects prey species' behavior, even in the absence of a direct threat, but human-induced environmental change may disturb ecologically significant predator–prey interactions. Here, we propose various ways in which knowledge of antipredator tactics, behavioral risk effects, and primate–predator interactions could assist in identifying human-caused disruption to natural systems. Using behavior to evaluate primate responses to the ongoing environmental change should be a potentially effective way to make species conservation more predictive by identifying issues before a more dramatic population declines. A key challenge here is that studies of predation on primates often use data collected via direct observations of habituated animals and human presence can deter carnivores and influence subjects' perception of risk. Hence, we also review various indirect data collection methods to evaluate their effectiveness in identifying where environmental change threatens wild species, while also minimizing observer bias.

KEYWORDS
antipredator behavior, conservation, human-induced rapid environmental change (HIREC), human-shield effect, primate

1 | INTRODUCTION

Predators influence their prey through both direct consumption and nonlethal "risk effects" on plastic phenotypic traits (Moll et al., 2017; Preisser, Bolnick, & Benard, 2005). In particular, the behavioral consequences of risk have received much attention from ecologists in recent decades (Creel & Christianson, 2008; Moll et al., 2017; Preisser et al., 2005). When prey animals perceive themselves to be under high risk, their responses can carry foraging and physiological costs that affect individual reproductive success (Creel & Christianson, 2008; Creel, Christianson, Liley, & Winnie, 2007). These costs can scale up to influence overall population density and demographics (Atkins et al., 2019; Creel & Christianson, 2008; Creel et al., 2007) and produce cascading effects on the wider ecosystem (Atkins et al., 2019; Laundré, Hernández, & Ripple, 2010). Despite the well-recognized importance of perceived risk in shaping prey behavior and ecology, the idea that fear as an emotional state can drive animal decision-making is relatively new in ecology (Brown, Laundré, & Gurung, 1999; Laundré et al., 2010). This contrasts with psychological research on nonhuman primates that have long acknowledged the importance of fear (e.g., Joslin, Fletcher, & Emlen, 1964). Yet, in comparison to other mammalian taxa, relatively few studies of primates have focused on nonlethal risk effects (Bidner, 2014). As such, we lack a thorough understanding of how predation risk shapes their behavior and ecology. This knowledge is important because anthropogenic change is known to be a major driver of the way prey animals perceive and respond to risk (Berger, 2007; Sih, Ferrari, & Harris, 2011).

Human-induced rapid environmental change (hereafter HIREC; Sih et al., 2011) including habitat modification, fragmentation, overexploitation, and the introduction of novel species can disrupt natural predator–prey relationships important to the integrity of ecological communities (Kareiva, 1987; Michalski & Peres, 2005). HIREC can

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obscure whether observed behaviors might be adaptive under a range of natural contexts or are more narrowly the result of plastic responses to specifically anthropogenic landscapes. Evidence indicates that species-typical predation rates in degraded or fragmented habitats could lead to primate extinction as predator- and prey-range overlap can increase when habitat loss causes both to be constrained to smaller areas (e.g., Irwin, Raharison, & Wright, 2009). Similarly, urbanization and fragmentation can concentrate less human-tolerant species in smaller natural areas, leading to more frequent interactions with predators (Parsons et al., 2019). Human hunting can also be thought of as a form of predation that threatens primate persistence as it can cause population declines even in continuous habitats, which is uncommon for other predators (Estrada et al., 2017; Reed & Bidner, 2004). Yet, whether fear of humans might result in behavioral "risk effects" in wild primates is relatively uncertain (Bidner, 2014). In other taxa, fear of hunters can lead to changes in movement and habitat use that affect foraging decisions (Lone et al., 2014), not only in prey species but also apex predators (Ngoprasert, Lynam, & Gale, 2007; Ordiz, Støen, Delibes, & Swenson, 2011). Exacerbating these problems are primates' relatively low reproductive rates and general inability to compensate for heightened levels of predation or hunting (Hill & Dunbar, 1998; Peres, 1990). Finally, because HIREC disproportionately affects large carnivores (Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012), it is relatively unknown how the loss of these species and decreased prey risk perception would affect wider ecological communities (Bidner, 2014).

Research on behavioral indicators of risk perception in primates should be useful for identifying situations in which HIREC has caused disturbance to predator–prey relationships and where habitats or human activities need to be managed (Caro, 2016; Wong & Candolin, 2015). Within primates, these behaviors often include alarm calling upon detecting danger (Stanford, 2002), choosing to utilize safer habitats at the expense of riskier but more resource-rich locations (Coleman & Hill, 2014; Cowlishaw, 1997; Willems & Hill, 2009), and monitoring the surrounding environment more intensely when/where they perceive more risk (Campos & Fedigan, 2014; Caro, 2005). Direct observation of habituated subjects is a commonly used method in field primatology (Williamson & Feistner, 2003) and these methods have looked for associations between antipredator behaviors and known risks from predators (Campos & Fedigan, 2014; Coleman & Hill, 2014; Willems & Hill, 2009). It is also possible to use these same behaviors as indicators of fear with information on conflict/hunting risk from humans (Bryson-Morrison, Tzanopoulos, Matsuzawa & Humle, 2017; Lindshield, Danielson, Rothman, & Pruetz, 2017). Yet, a direct observation also potentially biases antipredator studies because many carnivores actively avoid proximity to humans (Boesch, 1991; Isbell & Young, 1993; Smith et al., 2017; van Cleave et al., 2018). When comparatively tolerant prey species can perceive and exploit this increase in safety near

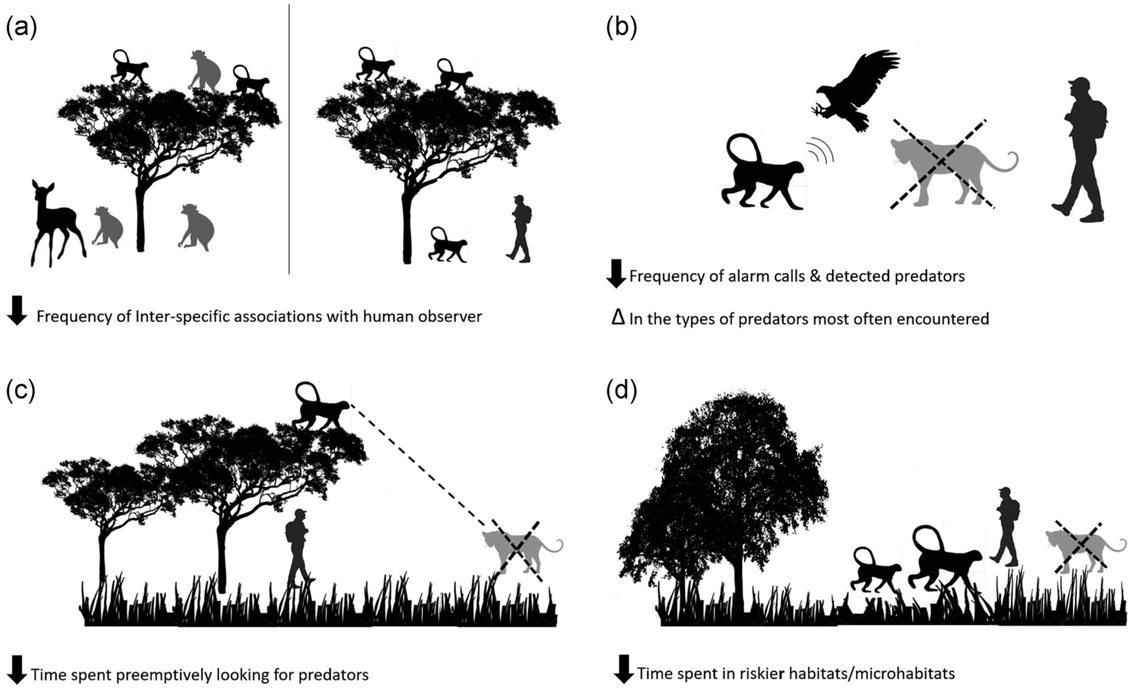

FIGURE 1 Predicted effects of human presence/direct observation on primate groups. (a) Human presence with habituated wildlife may produce changes in the types of species encountered and changes from prehabituation levels of inter-species association patterns when differences in habituation exist between species (different colors and shapes represent different species). (b) Certain guilds of predators may be more intolerant than others resulting in potentially erroneous conclusions about the importance of certain predators for a primate species ecology. (c) Over time, decreased predator encounter rates, whereas with human observers, could lead to decreased wariness and less time spent looking for predators. (d) Time spent in riskier habitats while under observation may also increase if subjects perceive themselves to be safer while in proximity to an observer

observers or even human infrastructure, it is known as the "human-shield effect" (Berger, 2007; Sarmento & Berger, 2017). Evidence suggests that at least some primates do perceive an increase in safety while under observation (Nowak, le Roux, Richards, Scheijen, & Hill, 2014). Consequently, methods that reduce or eliminate the possibility of a "human-shield" are important both for more accurately identifying where HIREC has altered predator–primate relationships and for understanding the basic behavioral ecology of wild primates (Figures 1 and 2).

Broader questions of how habitat change might affect predator–primate interactions and cooccurrence can be asked using data collected from remote sensing technologies like global positioning system (GPS) collars (Fehlmann et al., 2017), and wildlife-triggered camera traps (Boyer-Ontl & Pruetz, 2014; Farris, Karpanty, Ratelolahy, & Kelly, 2014) that do not require habituation. Coupling behavioral data with information on predator diets through scat analysis can also be useful for identifying predation by elusive carnivores that may be difficult to observe (Brockman, Godfrey, Dollar & Ratsirarson, 2008; Irwin et al., 2009). Field experiments using sensory cues from human hunters can indicate whether groups are subjected to hunting (Cagni, Sampaio, Ribeiro & Barros, 2011) without requiring habituation to observers. Responses to experimental predator cues can additionally indicate whether predator-naïve primates recognize dangerous cues before a reintroduction program (Gil-da-Costa, Palleroni, Hauser, Touchton, & Kelley, 2003).

Other methods that do not require habituation include flight initiation distance (FID) experiments that record the distance at which a prey animal will flee from an approaching threat (Cooper & Frederick, 2007). These experiments can be used as both a general indicator of risk perception and as an indicator of hunting pressure (when used with an approaching human) by comparing the response of animals in well-protected areas to those in locations that might be experiencing poaching or hunting (Donadio & Buskirk, 2006). Finally, the widely used method of giving-up density (GUD) experiments, in which researchers manipulate the amount of food in a foraging patch to indicate trade-offs between foraging and other activities, has been used to identify differences in perceived risk between habitats (Bedoya-Perez, Carthey, Mella, McArthur, & Banks, 2013). Animals are predicted to cease foraging earlier and leave more food behind in risky habitats than in safer areas. The results of these experiments can provide indirect evidence that anthropogenic change alters risk perception (Nowak, Hill, Wimberger, & le Roux, 2016; Nowak, Richards, le Roux, & Hill, 2016).

Critically assessing which methods are best for minimizing anthropogenic bias is important both for researchers studying fundamental behavioral biology (Caro & Sherman, 2011; Hockings et al., 2015) and for those aiming to conserve wild species. In this review, we discuss some of the ways in which primate antipredator behaviors might be used to assess human impacts on wild populations. We also contrast available methodologies with the goal of highlighting those most useful for understanding adverse anthropogenic disturbance.

2 | METHODS

We conducted extensive literature searches between December 2017–2018 on Google Scholar and Web of Knowledge using combinations of derivatives of the terms: predator/predation, antipredator, risk, prey, habitat, carnivore, and primate with the aim of investigating the most common methods for studying predation on primates. We also aimed to assess whether researchers used knowledge of antipredator strategies for conservation or for identifying where populations might be suffering from HIREC. Therefore, these searches were then repeated with derivatives of the terms: human, anthropogenic, conservation, threatened, extinct, and hunt. Finally, we noted the methods used in these studies and repeated our searches

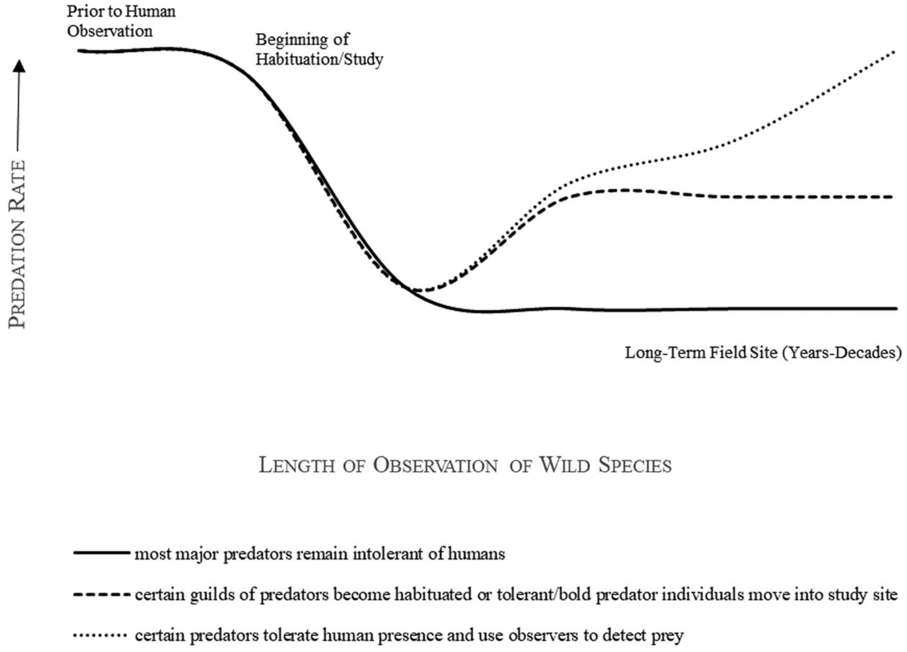

FIGURE 2 Hypothetical effects of direct observation on predation rates of habituated primate groups. Predators may remain intolerant of researchers for the duration of the study and avoid hunting individuals within a habituated study group. Certain guilds may become more habituated to human presence over time or bolder individuals that are more tolerant of people may eventually move into a study location. This may be less likely to occur if predator species are under hunting pressure from humans

with combinations of the terms: vigilance, alarm call, experiment, playback, predator cue, GPS, remote sense, camera trap, and predator diet. We also examined the references cited by each study as well as review articles on relevant topics (e.g., Allan & Hill, 2018; Bidner, 2014; Boinski, Treves, & Chapman, 2000; Fichtel, 2012; Isbell, 1994; Janson, 1998; Stanford, 2002) but did not include reviews, meta-analyses, simulation studies, or published abstracts in the total. We excluded papers where researchers studied a presumed antipredator behavior when the focus of the study was the risk of infanticide or within-species competition (e.g., vigilance and social monitoring). We additionally noted while reading these studies whether the research was conducted on subjects habituated to humans and plotted these data to infer whether this practice might be declining with new remote sensing technologies (GPS/radio collars, camera traps, etc.) or other methods that do not require direct observation. We expect our results are representative but not exhaustive of the primate predation literature. A limitation of this search is that wildlife managers may not publish reports on their activities in academic journals, and thus, we may not have included relevant examples from non-peer-reviewed sources.

3 | RESULTS

In total, we found 222 studies focused on primate antipredator behaviors published between 1977 and 2018 (S1). Most of the studies (188/222) used direct observation of subjects that were tolerant of human presence (~85%) but the proportion using direct observation declined over time (Figure 3). Several recent studies used alternative methods including GPS data from collared primates and/or their predators (Adams & Kitchen, 2018; Bidner, Matsumoto-Oda, & Isbell, 2018; Isbell & Bidner, 2016; Isbell, Bidner, van Cleave, Matsumoto-Oda, & Crofoot, 2018), camera traps (Boyer-Ontl & Pruetz, 2014; Farris et al., 2014; Isbell & Bidner, 2016), or predator scats for dietary analysis (Dollar, Ganzhorn, & Goodman, 2007; Irwin et al., 2009; Jooste, Pitman, van Hoven, & Swanepoel, 2012; Lenz & dos Reis, 2011; McGraw, Cooke, & Shultz, 2006; Shultz & Dunbar, 2006; Shultz, Noë, McGraw, & Dunbar, 2004). For example, Isbell et al. (2018) were able to identify encounters between GPS-collared predators and primates without human interference using predator and prey spatial coordinates to determine when and where species interacted. Camera traps also allowed researchers to collect behavioral data without direct observation (Boyer-Ontl & Pruetz, 2014; Farris et al., 2014). Finally, predator diets, coupled with knowledge of species-typical antipredator traits, enabled researchers to identify characteristics that increase vulnerability to predation (Shultz et al., 2004). These studies tended to cite potential bias or interference from human observers as a reason for using these types of data, but none of them explicitly tested predictions about a "human-shield effect" that has been more extensively investigated in other taxa.

Field experiments also tended to keep human observers out of sight from subjects while using playbacks of predator sounds, visual predator cues, or artificial foraging patches (Arnold & Zuberbühler, 2006, 2013; Emerson & Brown, 2012; Emerson, Brown, & Linden, 2011; Makin, Payne, Kerley, & Shrader, 2012). Predator experiments using sensory cues (visual models, playbacks, etc.) were the most common type of experiment, whereas a smaller number of more recent studies made use of GUD and one used FID (Figure 4).

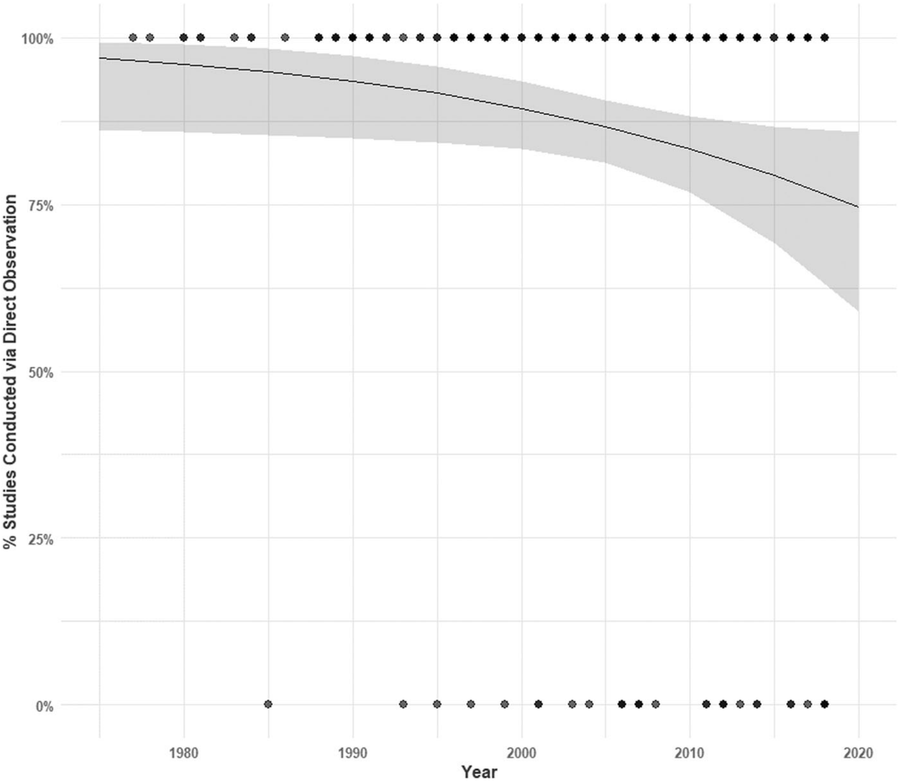

FIGURE 3 Percentage of sampled studies using direct observation of habituated subjects over the sampled years. We found the incidence of articles using direct observation slightly declined over time ($\beta = -.0442$, SE = ± 0.0246) using a binomial model adjusted for varying numbers of sampled articles per year

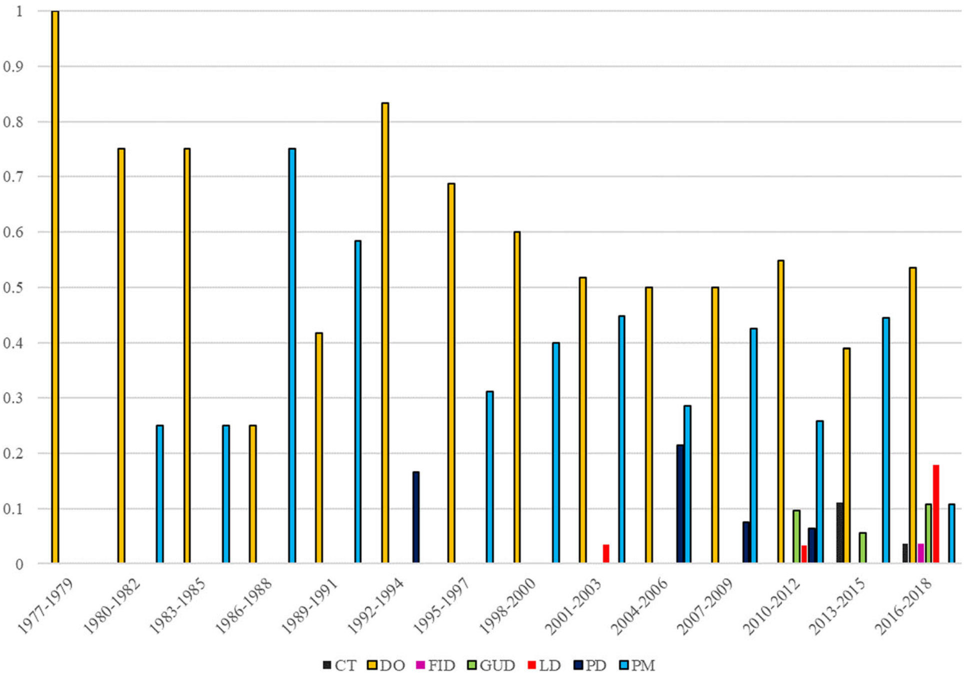

FIGURE 4 Proportion of studies using reviewed methods. CT, camera trapping; DO, direct observation; FID, flight initiation distance experiment; GUD, giving-up density experiment; LD, remotely sensed movement data from radio or GPS (global positioning system) collars; PD, predator diet information; PM, experiments using predator/hunter sensory cues

Of the total 222, 21 studies (~9.45%) were explicitly designed to address HIREC or species conservation (Table 1). Bryson-Morrison et al. (2017) and Lindshield et al. (2017) used direct observation of western chimpanzees (*Pan troglodytes verus*) to assess whether fear of humans might drive habitat use or foraging decisions. Specifically, Bryson-Morrison et al. used information about habitat-level differences in risk and examined whether this corresponded with utilization and activity budgets. The authors found that animals preferred to forage further from potentially risky cultivated fields but did not actively avoid roads or human paths where the risk of conflict was high. Lindshield et al. also used direct observation but measured feeding rates and vigilance behaviors along with information on food availability. They found that subjects tended to react fearfully to the immediate presence of locals and increased their party size in anthropogenic habitats, although location-specific variation in risk did not seem to predict the likelihood of using a particular feeding patch. In both cases, it is uncertain whether habituation to observers could have resulted in decreased fearfulness of other humans. We also included in this category studies by Teelen (2008) and Watts and Amsler (2013). Though not explicitly related to humans, these studies used data from direct observation of chimpanzee hunting to investigate whether this natural predatory behavior could be unsustainable for their preferred primate prey, and were thus relevant to conservation.

Studies relevant to conservation or HIREC also included those using remotely sensed data. Fehlmann et al. (2017) used GPS collars on adult male baboons living near Cape Town, South Africa, where rangers employed by the city actively deter baboons looking for anthropogenic food sources in urban areas or farms. Baboon activity levels (measured via attached accelerometers) were much higher in areas where the risk of being chased by a ranger was high. Brockman et al. (2008) and Irwin et al. (2009) combined lemur behavioral data with information on predator diet selection using scats. Brockman et al. specifically focused on exotic predators and found evidence that they were feeding on wild lemurs, whereas Irwin et al. found evidence that fragmentation might put lemurs at risk of local extinction through predation. Finally, Farris et al. (2014) used camera traps to monitor lemur–predator cooccurrence across a variety of habitat types with varying levels of fragmentation. The authors found that introduced predators and humans were more active in fragmented forests compared with continuous forests, whereas lemurs and native predators more active in continuous habitat.

Thirteen of the 21 studies that focused on HIREC/conservation used field experiments. These included simulated threats from hunters to gauge if antipredator behaviors towards humans could provide information on hunting pressure (Bshary, 2001; Croes et al., 2007; Papworth, Milner-Gulland, & Slocombe, 2013) and all three found evidence in support. Four studies used artificial foraging patches in the form of GUD experiments to investigate how human presence or human activities could affect primate risk perception (Nowak et al., 2014; Nowak, Hill, et al., 2016; Nowak, Richards, et al., 2016; Nowak, Wimberger, Richards, Hill, & le Roux, 2017). Nowak, Hill, et al. (2016) and Nowak et al. (2017) found evidence that Samango monkey (*Cercopithecus albogularis*) foraging behavior was sensitive to anthropogenic risk. GUD experiments in a more natural habitat conducted following Samango live-trapping indicated that habituated animals were unlikely to show a

TABLE 1 Methods of monitoring antipredator behaviors and primate–predator interactions used in reviewed studies for investigating the human-induced rapid environmental change (HIREC) or species conservation

Topic/concern	Method of investigation	Citation
Anthropogenic influences on risk perception (hunting, human-shields, and conflict with humans)	Field experiments—visual/auditory cues from humans	Bshary (2001); Croes et al. (2007); Papworth, Milner-Gulland, and Slocombe (2013)
	Field experiments—giving-up densities	Nowak, le Roux, Richards, Scheijen, and Hill (2014), Nowak, Hill, Wimberger, and le Roux (2016); Nowak, Richards, le Roux, and Hill (2016); Nowak, Wimberger, Richards, Hill, and le Roux (2017)
	GPS (global positioning system)/movement data	Fehlmann et al. (2017)
	Observation of risk-sensitive behaviors	Bryson-Morrison et al. (2017); Lindshield, Danielson, Rothman, and Pruetz (2017)
	Field experiments—flight initiation distance	Mikula, Šaffa, Nelson, and Tryjanowski (2018)
Overpredation or alteration to predation rates (invasive predators and altered habitat)	Predator diets (scat or known kills)	Brockman et al. (2008); Irwin, Raharison, and Wright (2009)
	Camera traps—cooccurrence or spatial/temporal avoidance of predators	Farris, Karpanty, Ratelolahy, and Kelly (2014)
	Direct observation of habituated predators	Teelen (2008); Watts and Amsler (2013)
Predator recognition abilities (reintroduction or translocation of primates or predators)	Field experiments—real or simulated cues from potential predators	Cagni et al. (2011); Friant, Campbell, and Snowdon (2008); Gil-da-Costa, Palleroni, Hauser, Touchton, and Kelley (2003); Gil-da-Costa (2007); Sündermann, Scheumann, and Zimmermann (2008)

sustained fear response to researcher equipment once trapping was complete (Nowak, Richards, et al., 2016). Habituated subjects also tended to forage more on the ground from GUD patches, indicating that observers might decrease subjects' perception of risk from terrestrial predators (Nowak et al., 2014). One study attempted to measure variation in risk perception using FID experiments with an approaching human observer and found that urban-dwelling vervet monkeys (*Chlorocebus pygerythrus*) delayed fleeing from an approaching human compared with individuals found in rural areas. The authors presumed that this difference was related to potentially lethal conflict over crop-raiding in agricultural areas leading to heightened perceptions of risk (Mikula, Šaffa, Nelson, & Tryjanowski, 2018). Finally, five studies tested captive or wild predator-naïve primate populations for their predator recognition abilities (Cagni et al., 2011; Friant, Campbell, & Snowdon, 2008; Gil-da-Costa, 2007; Gil-da-Costa et al., 2003; Sündermann, Scheumann, & Zimmermann, 2008). Results from these studies suggest that predator recognition is sometimes innate but often requires learning about predators and their cues.

4 | DISCUSSION

Although relatively little research uses primate antipredator behaviors for identifying when species are adversely affected by HIREC, we located a set of highly relevant studies focused on primate–predator interactions and antipredator behaviors. Their approaches included using antipredator behavior to gauge hunting pressure (Bshary, 2001; Croes et al., 2007; Papworth et al., 2013), to investigate how primates deal with fear of (potentially lethal) conflict with humans (Bryson-Morrison et al., 2017; Fehlmann et al., 2017; Lindshield et al., 2017; Mikula et al., 2018), and/or to assess whether predator-naïve primates could discern whether an animal was dangerous (Cagni et al., 2011; Friant et al., 2008; Gil-da-Costa, 2007; Gil-da-Costa et al., 2003; Sündermann et al., 2008). Data on primate habitat use and risk-sensitive behaviors were also used to assess whether perceived risk varied between more natural or human-modified habitats (Nowak, Hill, et al., 2016; Nowak et al., 2017) and whether primates tended to avoid areas where native or exotic predators spent more time (Farris et al., 2014). Below we expand on the potential benefits and drawbacks of the various methods available for studying risk-sensitive behavior in primates with respect to understanding environmental change.

4.1 | Direct observation of habituated subjects

Habituation to observers and "human-shields" may compromise researchers' ability to assess how threats from humans or predators affect behavior and ecology of wild primate prey species. Researchers originally thought that this phenomenon was limited to humans deterring unhabituated predators rather than introducing behavioral changes in primate prey (Crofoot, Lambert, Kays, & Wikelski, 2010). However, evidence for a "human-shield" has been found in a variety of taxa (Atickem, Loe, & Stenseth, 2014; Berger, 2007; Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011; Nowak et al., 2014; Sarmento & Berger, 2017). How long this phenomenon persists likely depends on the types and tolerance of predator species present (Smith, Thomas, Levi, Wang, & Wilmers, 2018) and whether those individual predators tend to have negative or relatively neutral interactions with humans (Figure 2; Isbell & Young, 1993). Additional issues with direct observation include researcher assumptions about which behaviors are sensitive to perceived predation risk. Studies of vigilance have been criticized as numerous social and environmental factors can affect the behavioral markers researchers tend to record (Allan & Hill, 2018; Stanford, 2002; Treves, 2000). Though alarm calls may provide a more reliable indication of immediate risk perception, recorded spatial patterns may be relevant only when subjects are in proximity to observers. Finally, studies of anthropogenic risk focused on risk of conflict or of being hunted may also be biased because "behavioral spillover" could lead habituated primates to perceive potentially dangerous humans as less risky (Geffroy, Samia, Bessa, & Blumstein, 2015; Kasereka, Muhigwa, Shalukoma, & Kahekwa, 2006). Thus, we cannot assume that observer recorded patterns of risk-sensitive behavior will necessarily match up with the experience of unhabituated animals (Figure 1); the use of technologies and/or field experiments that do not require habituation may be preferable for most HIREC/conservation-related questions.

Notable exceptions to the problem of observer presence include studies of habituated chimpanzees hunting other primates (Stanford, 1995; Teelen, 2008; Watts & Amsler, 2013) and studies of carnivores that were tracked by observers (Zuberbühler, Jenny, & Bshary, 1999). These detailed observations have certainly advanced the study of primate–predator interactions. Yet, researchers should remain cautious about interpreting overall predation rates or spatial patterns of risk from these data. Previous studies have found that direct observation might affect how successful hunting chimpanzees are at killing prey species if unhabituated prey alarm call at approaching humans (Boesch, 1994). Conversely, if unhabituated prey associate humans with specific predators, they may learn to detect these cues earlier, leading to reduced hunting success. These studies are therefore useful for understanding basic behavioral ecology, but tracking predators likely has less utility for research on anthropogenic risk.

4.2 | Indirect and remote monitoring

4.2.1 | Movement data

Monitoring movement through GPS or radio collars is now widely used in animal ecology (Kays, Crofoot, Jetz, & Wikelski, 2015) and has become more common for studying primate behavior and primate–predator interactions in recent years (Figure 3). Although only one study reviewed used remotely monitored collar data to investigate how primates might respond to risk from humans (Fehlmann et al., 2017), numerous questions about habitat alteration or anthropogenic effects on risk perception could be investigated with the help of these technologies. These might include investigations into how predator–primate movement and interaction frequency might differ between continuous versus fragmented or degraded habitats. Location data can also be used to assess how human activity or infrastructure might alter space-use in both primates and their predators. Thus far, many studies have investigated similar questions in large carnivores (Ngoprasert et al., 2007; Ordiz et al., 2011; van Cleave et al., 2018), but monitoring both predator and prey could indicate whether areas of high human activity function as "shields" for primates. This might especially be true where predators are subject to conflict or trophy hunting (Ordiz et al., 2011).

Employing similar methods in areas where primates are at risk from hunters could help explore how risk effects from human predation affect overall movement and whether subjects preferentially utilize locations and (micro)habitats further from human settlements. Coupling this with vegetation data on resource availability and habitat permeability to predict how anthropogenic risk would influence movement or utilization would mimic studies of predator-induced "landscapes of fear" (Laundré et al., 2010; Willems & Hill, 2009) and would be novel for wild primates. In areas where hunting of primates is legal and hunters themselves are willing to assist researchers, information about hunter tactics and movements might also provide useful information for managers seeking to protect wild species through a better understanding of which microhabitats might serve as refuge from hunters. In a study of human movement ecology, Papworth, Bunnefeld, Slocombe, and Milner-Gulland (2012) asked human subjects to carry handheld GPS devices during hunting and gathering activities and found that methods used for estimating habitat selection and resource use in wildlife could be effectively applied to humans. Though the authors explicitly examined human behavior, similar methods could be used in conjunction with data from populations of wild primates already studied with GPS collars. A knowledge of where and when human–primate interactions tend to be lethal could inform managers about the types of habitats that are important for restoration or conservation and that could ensure more sustainable hunting. A final application of using remotely sensed movement data for measuring risk-sensitive behavior could be to assess observer effects on already studied populations to explore whether resource selection, landscape utilization, and activity patterns differ when groups are under continuous observation compared to periods with little or no proximity to researchers.

An important limitation of these methods is that they generally cannot estimate overall predation rates; researchers may underestimate the strength of antipredator behavior as encounters with uncollared predators (or humans not participating in a study) will go undetected. This can also be the case for encounters that occur between GPS fixes (Creel et al., 2013) and for primate species living in multipredator environments under risk from several predators simultaneously.

4.2.2 | Camera-trap data

Motion-sensitive camera traps are widely used for remotely collecting data on animal abundance and density and can provide estimates of cooccurrence between predators and prey. Though much of the camera-trap work focuses on estimating population sizes (Burton et al., 2015), they can be used for measuring behaviors such as temporal or spatial avoidance of competitors or of predators by prey (Farris et al., 2014; Niedballa, Wilting, Sollmann, Hofer, & Courtiol, 2019). Although camera traps have typically been used on terrestrial wildlife, recent studies have validated their use at ground level for semiterrestrial species (Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 2019) and, by placing cameras strategically along natural crossing points in forest strata, for arboreal primates (Gregory, Carrasco Rueda, Deichmann, Kolowski, & Alonso, 2014). In some instances, camera traps can provide data comparable to direct observation, including individual identities (McCarthy et al., 2019), as well as help researchers avoid the risks associated with habituating wild primates. For example, Boyer-Ontl and Pruetz (2014) used cameras to monitor cave use by unhabituated West African savannah chimpanzees. Their photos also indicated where chimpanzees and carnivores co-occurred on the landscape. Isbell and Bidner (2016) combined data from GPS-collared leopards and collared vervet monkeys with camera trap photographs to detect leopard visits to sleep sites. Future applications of these methods could include measuring primate occurrence data across a gradient of land types to determine whether areas of high human activity might serve as refuges from predators. Conversely, this approach could also be used to assess whether the fear of human hunting is associated with landscape-level patterns of species occurrence. Although we could not find any examples with primates, such studies have been conducted with other taxa (Muhly et al., 2011).

4.2.3 | Predator diets

Examining the hunting and dietary habits of the predators of primates is one way to study predation without human interference (Isbell, 1994). Knowledge of a primate species' behaviors coupled with this information can be useful for assessing relative predation vulnerability between populations or species. Irwin et al. (2009) and Brockman et al. (2008) both used these methods for inferring whether HIREC could alter predation on wild lemurs by native carnivores (Irwin et al.) through habitat alteration and the introduction of exotic wild cats (*Felis silvestris*; Brockman et al.). Prey remains within predator scat could be analyzed using morphological markers (e.g., hair cross-sections and bones) or by extracting fDNA. Of the two methods, morphological markers are more commonly used to identify prey items and are relatively inexpensive, but molecular methods coupled with Sanger or more recently developed high-throughput sequencing can help reduce uncertainty about both prey and predator identity (Monterroso et al., 2019). Future research should compare predator diet composition in areas with long-term research projects with nearby areas of similar community composition, but with relatively less human activity. This would provide needed information on whether spatial or temporal avoidance of humans might alter prey selection.

4.3 | Field experiments

4.3.1 | Cues from hunters or predators

Three of the reviewed studies using field experiments with cues from human hunters found evidence that primates respond to these with antipredator behaviors (Bshary, 2001; Croes et al., 2007; Papworth et al., 2013). The major implication of this result is that behavioral indicators might also be used to identify populations in need of additional protection when it is uncertain whether hunting/poaching is occurring, and this information should help managers decide where to allocate resources for protection of large reserves or parks. Testing differences between populations to responses to human presence, however, may be less useful if researchers make comparisons between unprotected areas and protected areas with high tourist or researcher activity. In these instances, researchers must be careful that the heightened "antipredator" behaviors they record in unprotected locations do not simply indicate a lack of experience with humans rather than differences in hunting/predation pressure. Nevertheless, there is evidence that some primates can distinguish between non-threatening and dangerous types of humans based on their behavior/appearance (Papworth et al., 2013). A new way of implementing these kinds of experiments is to couple camera traps with playback cues from hunters or predators using the Automated Behavioral Response system developed by Suraci et al. (2017). In their preliminary experiments, the authors successfully used speakers triggered by motion sensors to play sounds of human hunters at Bwindi Forest, Uganda, to gauge illegal hunting pressure without observer interference. This system has also allowed researchers studying cougar (*Puma concolor*) responses to anthropogenic sounds to measure whether fear of humans could alter their risk perception and predation behavior, resulting in a human-induced foraging cascade (Smith et al., 2017). This system could also be a powerful way of testing fear responses across a range of taxa going forward.

4.3.2 | Predator recognition experiments

How primates acquire knowledge about and respond appropriately to predators is an important area of research as reintroductions and translocations can lead predator-naïve primates to encounter unfamiliar predators. This problem will likely be exacerbated by altered species distributions due to climate change (Estrada et al., 2017). Across taxonomic groups, failure to fully account for how naïve prey may be unable to recognize and react to predator cues has contributed to the failure of many releases from captive-breeding programs (Sinclair et al., 1998). This problem was an impetus for studies of predator recognition in captive-born primate groups (Cagni et al., 2011; Friant et al., 2008; Sündermann et al., 2008) and studies of wild-born but predator-naïve primates (Gil-da-Costa, 2007; Gil-da-Costa et al., 2003). Prior identification of predator naïveté has allowed behavioral researchers to design methodologies for training captive prey prerelease (Moseby, Carthey, & Schroeder, 2015) or in-situ (West, Letnic, Blumstein, & Moseby, 2018) to limit excessive mortality. For similarly inexperienced prey dealing with exotic predators, some evidence suggests that those that have historically had to avoid similar types of predators and have potentially evolved the ability to recognize certain cues or features as dangerous are at less risk of extinction (Ehlman, Trimmer, & Sih, 2019). Testing whether this is true for various species of wild primates should help predict which are likely able to cope with new or invasive predators in the future.

4.3.3 | Flight initiation distance

Although most unhabituated animals are intolerant to humans, flight distance can indicate relative differences in perceived risk. This can be used as an indirect measure of the degree of disturbance, conflict, or hunting affecting different populations or groups of the same species (Boer, Breukelen, Hootsmans, & Wieren, 2004). These types of studies can be used for assessing how tourism in protected areas can lead to habituation or sensitization (Sutton & Heske, 2017). Increased flight distance over time or between populations can also indicate evidence for hunting/poaching or increased conflict (Donadio & Buskirk, 2006). Our literature search located only one primate FID study that focused on differences in vervet monkey FIDs between rural and urban settings and attempted to relate flight distance to group size, age–sex class, and habitat type (Mikula et al., 2018). Although valuable in highlighting the methodological approach, the study grouped data between sites without providing specific information on the relative danger from various threats (e.g., conflict with humans, predators, and hunting). Furthermore, unambiguous interpretations of the data were difficult because urban-dwelling groups were consistently smaller than their rural groups and potentially more tolerant to humans. Many other FID studies have similarly compared flight distances to an approaching observer between areas designated as “disturbed” and “undisturbed,” without accounting for the possibility that individuals or groups that are naturally more tolerant or bold across a variety of taxa might be better able to exploit areas with greater human activity (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). For example, yellow-bellied marmots (*Marmota flaviventris*) with more consistent human disturbance had lower FIDs, indicating those individuals had become more tolerant of humans (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013). The authors attributed this difference to habituation or spatial assortment based on personality characteristics. Increased flight distances could also be due to decreased energy costs of initiating flight earlier due to more easily available forage in urban areas (Møller et al., 2015). The latter may often be the case with primates living in anthropogenic habitats as they are often able to exploit energy-rich anthropogenic food sources (Brennan, Else, & Altmann, 1985).

Although not included in the literature review, Allan, Bailey, and Hill (in review) used FID methodology and found that individual habituated gray-footed chacma baboons (*Papio ursinus griseipes*) likely perceived an approaching observer more as a social threat than a predator. The authors also found that tolerance to an approaching human was highly distinct amongst individuals, and repeatable within individuals, suggesting that the process of habituation does not result in equal tolerance to a stimulus across a social group. This suggests that habituated subjects may not be appropriate targets for FID studies of predation risk. Though FID methods should be used by researchers aiming to measure how anthropogenic environmental change affects risk-sensitivity, these methods are best applied when detailed information on both the study site location(s) and characteristics of the study subjects are well understood.

4.3.4 | Giving-up densities

GUD methods have been used with wild primates to examine differences in perceived predation risk between microhabitats (Emerson et al., 2011; Makin et al., 2012) and risk from humans on foraging trade-offs (Nowak, Hill, et al., 2016; Nowak, Richards, 2016; Nowak et al. 2017). Nowak et al. (2014) used these methods with habituated animals and found that when not in proximity to an observer, individuals tended to forage less from the ground, suggesting the presence of a “human shield.” From a conservation standpoint, GUD experiments are likely to be most useful when they can serve as an indicator of habitat selection in anthropogenically altered environments in which human activity might alter food availability, predator density, or habitat structure (Bleicher, 2017). For example, GUDs have been used in non-primate taxa to assess which habitats serve as refuges (Carter & Bright, 2003) and to contrast foraging behavior in fragmented or degraded habitats with more pristine environments (Whelan & Jedlicka, 2007). However, GUDs have been criticized as a relatively coarse indicator of habitat quality as a high GUD can indicate both resource-rich environment and an area of high perceived predation risk. Thus, environment-specific attributes such as food availability or predator density need to be accounted for between-patch locations (Brown, 1988). An additional factor is that in social species, multiple individuals may access the same patch simultaneously. To avoid results being driven by bolder and/or more risk-insensitive individuals, patches should be spread out to reduce monopolization (Réale & Festa-Bianchet, 2003). Non-target species may also feed on artificial patches, but this might be overcome by introducing the setup to target animals in stages, allowing them to learn that patches contain food while slowly increasing the complexity of the design. Furthermore, using camera traps or animal-triggered video cameras in place of direct observation could help remove potential “human-shield” bias (Bedoya-Perez et al., 2013; Emerson et al., 2011; Nowak et al., 2014).

5 | CONCLUSIONS

Global change is relevant to behavioral biology because many long-term field sites focused on the adaptive significance of behavior will likely be compromised by extensive environmental change (Caro & Sherman, 2011) and this includes long-term studies of primates (Hockings et al., 2015). Although much of the order's inherent behavioral flexibility may help certain species survive alongside humans (McLennan, Spagnoletti, & Hockings, 2017), the environments encountered in the next century may be very different from those that most living species experienced over the course of their evolution (Hockings et al., 2015). Among these changes, numerous examples indicate that human activities can alter natural predator–primate relationships.

Each method reviewed here, has inherent benefits and drawbacks that are likely to vary between specific study species, populations, and habitats. Direct observation of risk-sensitive behaviors may be the most logistically workable method for a wide range of primate researchers, but it does not necessarily produce ecologically realistic results. The alternative methodologies we discuss here will often constrain the types of questions researchers can ask and provide less detail about individual subjects, but likely provide more accurate data on predator–primate relationships. Given what we currently know about the ways in which humans can impact wildlife risk perception, we believe these alternatives can benefit both basic primate behavioral ecology and ultimately contribute to species conservation.

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REFERENCES

Adams, D. B., & Kitchen, D. M. (2018). Experimental evidence that titi and saki monkey alarm calls deter an ambush predator. *Animal behaviour*, *145*, 141–147.

Allan, A. T., & Hill, R. A. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. *American Journal of Physical Anthropology*, *165*, 4–22. https://doi.org/10.1002/ajpa.2338

Atickem, A., Loe, L. E., & Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain nyala. *Ethology*, *120*(7), 715–725. https://doi.org/10.1111/eth.12242

Atkins, J. L., Long, R. A., Pansu, J., Daskin, J. H., Potter, A. B., Stalmans, M. E., … Pringle, R. M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*, *364*(6436), 173–177. https://doi.org/10.1126/science.aau3561

Arnold, K., & Zuberbühler, K. (2006). The alarm-calling system of adult male putty-nosed monkeys, Cercopithecus nictitans martini. *Animal behaviour*, *72*(3), 643–653.

Arnold, K., & Zuberbühler, K. (2013). Female putty-nosed monkeys use experimentally altered contextual information to disambiguate the cause of male alarm calls. *PLoS One*, *8*(6), e65660.

Bedoya-Perez, M. A., Carthey, A. J., Mella, V. S., McArthur, C., & Banks, P. B. (2013). A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology*, *67*(10), 1541–1553. https://doi.org/10.1007/s00265-013-1609-3

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*(6), 620–623. https://doi.org/10.1098/rsbl.2007.0415

Bidner, L. R. (2014). Primates on the menu: Direct and indirect effects of predation on primate communities. *International Journal of Primatology*, *35*(6), 1164–1177. https://doi.org/10.1007/s10764-014-9797-x

Bidner, L. R., Matsumoto-Oda, A., & Isbell, L. A. (2018). The role of sleeping sites in the predator-prey dynamics of leopards and olive baboons. *American journal of primatology*, *80*(12), e22932.

Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ (Corta Madera, CA and London)*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Boer, H. Y. D., Breukelen, L. V., Hootsmans, M. J., & Wieren, S. E. V. (2004). Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biology*, *10*(1), 35–41. https://doi.org/10.2981/wlb.2004.007

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, *117*, 220–242. https://doi.org/10.1163/156853991X00544

Boesch, C. (1994). Chimpanzees-red colobus monkeys: A predator-prey system. *Animal Behaviour*, *47*(5), 1135–1148. https://doi.org/10.1006/anbe.1994.1152

Boinski, S., Treves, A., & Chapman, C. A. (2000). A critical evaluation of the influence of predators on primates: Effects on group travel, *On the move: How and why animals travel in groups* (pp. 43–72). Chicago, IL: University of Chicago Press.

Boyer-Ontl, K. M., & Pruetz, J. D. (2014). Giving the forest eyes: The benefits of using camera traps to study unhabituated chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *International Journal of Primatology*, *35*(5), 881–894. https://doi.org/10.1007/s10764-014-9783-3

Brennan, E. J., Else, J. G., & Altmann, J. (1985). Ecology and behaviour of a pest primate: Vervet monkeys in a tourist-lodge habitat. *African Journal of Ecology*, *23*(1), 35–44. https://doi.org/10.1111/j.1365-2028.1985.tb00710

Brockman, D. K., Godfrey, L. R., Dollar, L. J., & Ratsirarson, J. (2008). Evidence of invasive Felis silvestris predation on Propithecus verreauxi at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *29*(1), 135–152.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*(1), 37–47. https://doi.org/10.1007/BF00395696

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Bshary, R. (2001). Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behavioral Ecology and Sociobiology*, *50*(3), 251–256. https://doi.org/10.1007/s002650100354

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., … Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675–685. https://doi.org/10.1111/1365-2664.12432

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and habitat use of chimpanzees (Pan troglodytes verus) in the anthropogenic landscape of Bossou, Guinea, West Africa. *International journal of primatology*, *38*(2), 282–302.

Cagni, P., Sampaio, A. C., Ribeiro, N. B., & Barros, M. (2011). Immediate, but no delayed, behavioral response to a snake model by captive black tufted-ear marmosets. *Behavioural processes*, *87*(3), 241–245.

Campos, F. A., & Fedigan, L. M. (2014). Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology*, *25*(3), 477–486. https://doi.org/10.1093/beheco/aru005

Cappelle, N., Després-Einspenner, M. L., Howe, E. J., Boesch, C., & Kühl, H. S. (2019). Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology*, *81*(3), e22962. https://doi.org/10.1002/ajp.22962

Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.

Caro, T. (2016). Behavior and conservation, conservation and behavior. *Current Opinion in Behavioral Sciences*, *12*, 97–102. https://doi.org/10.1016/j.cobeha.2016.09.008

Caro, T., & Sherman, P. W. (2011). Endangered species and a threatened discipline: Behavioural ecology. *Trends in Ecology & Evolution*, *26*(3), 111–118. https://doi.org/10.1016/j.tree.2010.12.008

Carter, S. P., & Bright, P. W. (2003). Reedbeds as refuges for water voles (*Arvicola terrestris*) from predation by introduced mink (*Mustela vison*). *Biological Conservation*, *111*(3), 371–376. https://doi.org/10.1016/S0006-3207(02)00305-1

van Cleave, E. K., Bidner, L. R., Ford, A. T., Caillaud, D., Wilmers, C. C., & Isbell, L. A. (2018). Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in central Kenya. *Biological Conservation*, *226*, 224–237. https://doi.org/10.1016/j.biocon.2018.08.003

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Cooper, W. E., Jr, & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, *244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, *53*(4), 667–686. https://doi.org/10.1006/anbe.1996.0298

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, *23*(4), 194–201. https://doi.org/10.1016/j.tree.2007.12.004

Creel, S., Christianson, D., Liley, S., & Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science*, *315*(5814), 960–960. https://doi.org/10.1126/science.1135918

Creel, S., Winnie, J. A., Jr, & Christianson, D. (2013). Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution*, *3*(16), 5189–5200. https://doi.org/10.1002/ece3.896

Croes, B. M., Laurance, W. F., Lahm, S. A., Tchignoumba, L., Alonso, A., Lee, M. E., … Buij, R. (2007). The influence of hunting on antipredator behavior in Central African monkeys and duikers. *Biotropica*, *39*(2), 257–263. https://doi.org/10.1111/j.1744-7429.2006.00247.x

Crofoot, M. C., Lambert, T. D., Kays, R., & Wikelski, M. C. (2010). Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Animal Behaviour*, *80*(3), 475–480. https://doi.org/10.1016/j.anbehav.2010.06.006

Dollar, L., Ganzhorn, J. U., & Goodman, S. M. (2007). Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest of western Madagascar. In S. Gursky-Doyen & K. A. I. Nekaris (Eds.), *Primate anti-predator strategies* (pp. 63–76). Boston, MA: Springer.

Donadio, E., & Buskirk, S. W. (2006). Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biological Conservation*, *127*(2), 139–145. https://doi.org/10.1016/j.biocon.2005.08.004

Ehlman, S. M., Trimmer, P. C., & Sih, A. (2019). Prey responses to exotic predators: effects of old risks and new cues. *The American Naturalist*, *193*(4), 575–587.

Emerson, S. E., & Brown, J. S. (2012). Using giving-up densities to test for dietary preferences in primates: An example with Samango monkeys (*Cercopithecus (nictitans) mitis erythrarchus*. *International Journal of Primatology*, *33*(6), 1420–1438. https://doi.org/10.1007/s10764-012-9631-2

Emerson, S. E., Brown, J. S., & Linden, J. D. (2011). Identifying Sykes' monkeys', *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Animal Behaviour*, *81*(2), 455–462. https://doi.org/10.1016/j.anbehav.2010.11.018

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., … Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946. https://doi.org/10.1126/sciadv.1600946

Farris, Z. J., Karpanty, S. M., Ratelolahy, F., & Kelly, M. J. (2014). Predator–primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in northeastern Madagascar. *International Journal of Primatology*, *35*(5), 859–880. https://doi.org/10.1007/s10764-014-9786-0

Fehlmann, G., O'Riain, M. J., Kerr-Smith, C., Hailes, S., Luckman, A., Shepard, E. L., & King, A. J. (2017). Extreme behavioural shifts by baboons exploiting risky, resource-rich, human-modified environments. *Scientific Reports*, *7*(1), 15057. https://doi.org/10.1038/s41598-017-14871-2

Fichtel, C. (2012). Predation. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 169–194). Chicago, IL: University of Chicago Press.

Friant, S. C., Campbell, M. W., & Snowdon, C. T. (2008). Captive-born cotton-top tamarins (*Saguinus oedipus*) respond similarly to vocalizations of predators and sympatric nonpredators. *American Journal of Primatology*, *70*(7), 707–710. https://doi.org/10.1002/ajp.20552

Geffroy, B., Samia, D. S., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, *30*(12), 755–765. https://doi.org/10.1016/j.tree.2015.09.010

Gil-da-Costa, R. (2007). Howler monkeys and harpy eagles: A communication arms race. In S. Gursky-Doyen & K. A. I. Nekaris (Eds.), *Primate anti-predator strategies* (pp. 289–307). Boston, MA: Springer.

Gil-da-Costa, R., Palleroni, A., Hauser, M. D., Touchton, J., & Kelley, J. P. (2003). Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*(1515), 605–610. https://doi.org/10.1098/rspb.2002.2281

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., & Alonso, A. (2014). Arboreal camera trapping: Taking a proven method to new heights. *Methods in Ecology and Evolution*, *5*(5), 443–451. https://doi.org/10.1111/2041-210X.12177

Hill, R. A., & Dunbar, R. I. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour*, *135*, 411–430. https://doi.org/10.1163/156853998793066195

Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W., … Wilson, M. L. (2015). Apes in the Anthropocene: Flexibility and survival. *Trends in Ecology & Evolution*, *30*(4), 215–222. https://doi.org/10.1016/j.tree.2015.02.002

Irwin, M. T., Raharison, J. L., & Wright, P. C. (2009). Spatial and temporal variability in predation on rainforest primates: Do forest fragmentation and predation act synergistically? *Animal Conservation*, *12*(3), 220–230. https://doi.org/10.1111/j.1469-1795.2009.00243

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L. A., & Bidner, L. R. (2016). Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to leopards (*Panthera pardus*) function as a predator deterrent. *Behaviour*, *153*(5), 591–606. https://doi.org/10.1163/1568539X-00003365

Isbell, L. A., Bidner, L. R., van Cleave, E. K., Matsumoto-Oda, A., & Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, *118*, 1–13. https://doi.org/10.1016/j.jhevol.2018.02.003

Isbell, L. A., & Young, T. P. (1993). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour*, *45*, 1233–1235. https://doi.org/10.1006/anbe.1993.1145

Janson, C. H. (1998). Testing the predation hypothesis for vertebrate sociality: Prospects and pitfalls. *Behaviour*, *135*(4), 389–410. https://doi.org/10.1163/156853998793066177

Jooste, E., Pitman, R. T., van Hoven, W., & Swanepoel, L. H. (2012). Unusually high predation on chacma baboons (*Papio ursinus*) by female leopards (*Panthera pardus*) in the Waterberg Mountains, South Africa. *Folia Primatologica*, *83*(3-6), 353–360. https://doi.org/10.1159/000339644

Joslin, J., Fletcher, H., & Emlen, J. (1964). A comparison of the responses to snakes of lab-and wild-reared rhesus monkeys. *Animal Behaviour*, *12*(2-3), 348–352. https://doi.org/10.1016/0003-3472(64)90023-5

Kareiva, P. (1987). Habitat fragmentation and the stability of predator–prey interactions. *Nature*, *326*(6111), 388–390. https://doi.org/10.1038/326388a0

Kasereka, B., Muhigwa, J. B. B., Shalukoma, C., & Kahekwa, J. M. (2006). Vulnerability of habituated Grauer's gorilla to poaching in the Kahuzi-Biega National Park, DRC. *African Study Monographs*, *27*(1), 15–26. https://doi.org/10.1.1.491.9736

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *Open Ecology Journal*, *3*, 1–7. https://doi.org/0.7717/peerj.3772

Lenz, B. B., & dos Reis, A. M. (2011). Harpy eagle-primate interactions in the central Amazon. *The Wilson Journal of Ornithology*, *123*(2), 404–408. https://doi.org/10.1676/10-171.1

Lindshield, S., Danielson, B. J., Rothman, J. M., & Pruetz, J. D. (2017). Feeding in fear? How adult male western chimpanzees (*Pan troglodytes verus*) adjust to predation and savanna habitat pressures. *American Journal of Physical Anthropology*, *163*(3), 480–496. https://doi.org/10.1002/ajpa.23221

Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D., Odden, J., Remmen, J., & Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: Roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, *123*(6), 641–651. https://doi.org/10.1111/j.1600-0706.2013.00938

Makin, D. F., Payne, H. F., Kerley, G. I., & Shrader, A. M. (2012). Foraging in a 3-D world: How does predation risk affect space use of vervet monkeys? *Journal of Mammalogy*, *93*(2), 422–428. https://doi.org/10.1644/11-MAMM-A-115.1

McCarthy, M. S., Després-Einspenner, M. L., Farine, D. R., Samuni, L., Angedakin, S., Arandjelovic, M., … Langergraber, K. E. (2019). Camera traps provide a robust alternative to direct observations for constructing social networks of wild chimpanzees. *Animal Behaviour*, *157*, 227–238. https://doi.org/10.1016/j.anbehav.2019.08.008

McGraw, W. S., Cooke, C., & Shultz, S. (2006). Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *American Journal of Physical Anthropology*, *131*(2), 151–165. https://doi.org/10.1002/ajpa.20420

McLennan, M. R., Spagnoletti, N., & Hockings, K. J. (2017). The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *International Journal of Primatology*, *38*(2), 105–121. https://doi.org/10.1007/s10764-017-9962-0

Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, *124*(3), 383–396. https://doi.org/10.1016/j.biocon.2005.01.045

Mikula, P., Šaffa, G., Nelson, E., & Tryjanowski, P. (2018). Risk perception of vervet monkeys *Chlorocebus pygerythrus* to humans in urban and rural environments. *Behavioural Processes*, *147*, 21–27. https://doi.org/10.1016/j.beproc.2017.12.011

Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., … Montgomery, R. A. (2017). The many faces of fear: A synthesis of the methodological variation in characterizing predation risk. *Journal of Animal Ecology*, *86*(4), 749–765. https://doi.org/10.1111/1365-2656.12680

Monterroso, P., Godinho, R., Oliveira, T., Ferreras, P., Kelly, M. J., Morin, D. J., … Mills, L. S. (2019). Feeding ecological knowledge: The underutilised power of faecal DNA approaches for carnivore diet analysis. *Mammal Review*, *49*(2), 97–112. https://doi.org/10.1111/mam.12144

Moseby, K., Carthey, A., & Schroeder, T. (2015). The influence of predators and prey naivety on reintroduction success: Current and future directions. In D. Armstrong, M. Hayward, D. Moro & P. Seddon (Eds.), *Advances in reintroduction biology of Australian and New Zealand fauna* (pp. 29–42). Clayton, Australia: CSIRO Publishing.

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLOS One*, *6*(3), e17050. https://doi.org/10.1371/journal.pone.0017050

Møller, A. P., Tryjanowski, P., Díaz, M., Kwieciński, Z., Indykiewicz, P., Mitrus, C., … Polakowski, M. (2015). Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behavioral Ecology*, *26*(3), 861–865. https://doi.org/10.1093/beheco/arv024

Ngoprasert, D., Lynam, A. J., & Gale, G. A. (2007). Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx*, *41*(3), 343–351. https://doi.org/10.1017/S0030605307001102

Niedballa, J., Wilting, A., Sollmann, R., Hofer, H., & Courtiol, A. (2019). Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote Sensing in Ecology and Conservation*, *5*(3), 272–285. https://doi.org/10.1002/rse2.107

Nowak, K., Hill, R. A., Wimberger, K., & le Roux, A. (2016). Risk-taking in Samango monkeys in relation to humans at two sites in South Africa. In K. M. Dore, E. P. Riley & A. Fuentes (Eds.), *Ethnoprimatology* (pp. 301–314). Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-30469-4_17

Nowak, K., Richards, S. A., le Roux, A., & Hill, R. A. (2016). Influence of live-capture on risk perceptions of habituated Samango monkeys. *Journal of Mammalogy*, *97*(5), 1461–1468. https://doi.org/10.1093/jmammal/gyw083

Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P., & Hill, R. A. (2014). Human observers impact habituated Samango monkeys' perceived landscape of fear. *Behavioral Ecology*, *25*(5), 1199–1204. https://doi.org/10.1093/beheco/aru110

Nowak, K., Wimberger, K., Richards, S. A., Hill, R. A., & Le Roux, A. (2017). Samango monkeys (*Cercopithecus albogularis labiatus*) manage risk in a highly seasonal, human-modified landscape in Amathole Mountains, South Africa. *International Journal of Primatology*, *38*(2), 194–206. https://doi.org/10.1007/s10764-016-9913-1

Ordiz, A., Støen, O. G., Delibes, M., & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, *166*(1), 59–67. https://doi.org/10.1007/s00442-011-1920-5

Papworth, S., Milner-Gulland, E. J., & Slocombe, K. (2013). Hunted woolly monkeys (*Lagothrix poeppigii*) show threat-sensitive responses to human presence. *PLOS One*, *8*(4), e62000. https://doi.org/10.1371/journal.pone.0062000

Papworth, S. K., Bunnefeld, N., Slocombe, K., & Milner-Gulland, E. J. (2012). Movement ecology of human resource users: Using net squared displacement, biased random bridges and resource utilization functions to quantify hunter and gatherer behaviour. *Methods in Ecology and Evolution*, *3*(3), 584–594. https://doi.org/10.1111/j.2041-210X.2012.00189

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., … Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, *54*, 1894–1904. https://doi.org/10.1111/1365-2664.13385

Peres, C. A. (1990). Effects of hunting on western Amazonian primate communities. *Biological Conservation*, *54*(1), 47–59. https://doi.org/10.1016/0006-3207(90)90041-M

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*(6), 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

Reed, K. E., & Bidner, L. R. (2004). Primate communities: Past, present, and possible future. *American Journal of Physical Anthropology*, *125*(S39), 2–39. https://doi.org/10.1002/ajpa.20153

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463–470. https://doi.org/10.1006/anbe.2003.2100

Samia, D. S., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, *6*, 8877. https://doi.org/10.1038/ncomms9877

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, *212*, 316–326. https://doi.org/10.1016/j.biocon.2017.06.032

Shultz, S., & Dunbar, R. I. M. (2006). Chimpanzee and felid diet composition is influenced by prey brain size. *Biology Letters*, *2*(4), 505–508. https://doi.org/10.1098/rsbl.2006.0519

Shultz, S., Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society B*, *271*(1540), 725–732. https://doi.org/10.1098/rspb.2003.2626

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*(2), 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P., & Newsome, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, *12*(3), 564–575. https://doi.org/10.1111/j.1523-1739.1998.97030.x

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1857), 20170433. https://doi.org/10.1098/rspb.2017.0433

Smith, J. A., Thomas, A. C., Levi, T., Wang, Y., & Wilmers, C. C. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos*, *127*(6), 890–901. https://doi.org/10.1111/oik.04592

Stanford, C. B. (1995). The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour*, *49*(3), 577–587. https://doi.org/10.1016/0003-3472(95)80191-X

Stanford, C. B. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, *23*(4), 741–757. https://doi.org/10.1023/A:1015572814388

Sündermann, D., Scheumann, M., & Zimmermann, E. (2008). Olfactory predator recognition in predator-naive gray mouse lemurs (*Microcebus murinus*). *Journal of Comparative Psychology*, *122*(2), 146–155. https://doi.org/10.1037/0735-7036.122.2.146

Suraci, J. P., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D. W., Smith, J. A., … Zanette, L. Y. (2017). A new automated behavioural response system to integrate playback experiments into camera trap studies. *Methods in Ecology and Evolution*, *8*(8), 957–964. https://doi.org/10.1111/2041-210X.12711

Sutton, N. M., & Heske, E. J. (2017). Effects of human state park visitation rates on escape behavior of white-tailed deer. *Human–Wildlife Interactions*, *11*(1), 12. https://doi.org/10.26077/ys7v-6n43

Teelen, S. (2008). Influence of chimpanzee predation on the red colobus population at Ngogo, Kibale National Park, Uganda. *Primates*, *49*(1), 41–49. https://doi.org/10.1007/s10329-007-0062-1

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*(6), 711–722. https://doi.org/10.1006/anbe.2000.1528

Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, *49*(1), 73–81. https://doi.org/10.1111/j.1365-2664.2011.02099.x

Watts, D. P., & Amsler, S. J. (2013). Chimpanzee-red colobus encounter rates show a red colobus population decline associated with predation by chimpanzees at Ngogo. *American Journal of Primatology*, *75*(9), 927–937.

West, R., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2018). Predator exposure improves anti-predator responses in a threatened mammal. *Journal of Applied Ecology*, *55*(1), 147–156. https://doi.org/10.1111/1365-2664.12947

Whelan, C. J., & Jedlicka, D. M. (2007). Augmenting population monitoring programs with behavioral indicators during ecological restorations. *Israel Journal of Ecology & Evolution*, *53*(3-4), 279–295. https://doi.org/10.1560/IJEE.53.3.279

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology*, *90*(2), 546–555. https://doi.org/10.1890/08-0765.1

Williamson, E. A., & Feistner, A. T. (2003). Habituating primates: Processes, techniques, variables and ethics. In J. M. Setchell (Ed.), *Field and laboratory methods in primatology: A practical guide* (pp. 25–39). Cambridge, UK: Cambridge University Press.

Wong, B., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3), 665–673. https://doi.org/10.1093/beheco/aru183

Zuberbühler, K., Jenny, D., & Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology*, *105*(6), 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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ORIGINAL ARTICLE

Influence of food availability, plant productivity, and indigenous forest use on ranging behavior of the endangered samango monkey (*Cercopithecus albogularis schwarzi*), in the Soutpansberg Mountains, South Africa

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Abstract

Understanding the determinants of ranging patterns in species susceptible to habitat fragmentation is fundamental for assessing their long-term adaptability to an increasingly human-dominated landscape. The aim of this study was to determine and compare the influence of ground-based food availability, remotely sensed plant productivity, and indigenous forest use on the ranging patterns of the endangered samango monkey (*Cercopithecus albogularis schwarzi*). We collected monthly ranging data on two habituated samango monkey groups, from February 2012 to December 2016, from our field site in the Soutpansberg Mountains, South Africa. We used linear mixed models to explore how food availability, plant productivity, and indigenous forest use influenced monthly ranging patterns, while controlling for group size, number of sample days and day length. We found that as more areas of high plant productivity (derived from remotely sensed EVI) were incorporated into the ranging area, both total and core monthly ranging areas decreased. In addition, both total ranging area and mean monthly daily path length decreased as more indigenous forest was incorporated into the ranging area. However, we found no effect of either ground-based food availability or remotely sensed plant productivity on ranging patterns. Our findings demonstrate the behavioral flexibility in samango monkey ranging, as samangos can utilize matrix habitat during periods of low productivity but are ultimately dependent on access to indigenous forest patches. In addition, we highlight the potential of using remotely sensed areas of high plant productivity to predict ranging patterns in a small ranging, forest-dwelling guenon, over ground-based estimates of food availability.

Key words: food availability, forest use, plant productivity, ranging patterns, remote sensing, samango monkey

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INTRODUCTION

Habitat loss and fragmentation are the most significant causes of global biodiversity loss (Fahrig 2003; Lindenmayer & Fischer 2006). Within forest biomes, loss and fragmentation of habitat has accelerated at an unprecedented rate due to the anthropogenic conversion of land for agriculture and urbanization (Haddad *et al.* 2015). Many species rely on continuous natural forest patches for foraging, reproduction, and shelter (Saunders *et al.* 1991; Fischer & Lindenmayer 2007). Fragmentation of these patches increases the likelihood of population declines through genetic isolation, microclimate change, decreased availability of resources, increased predation risk, and increased competition (Saunders *et al.* 1991; Fahrig 2003; Haddad *et al.* 2015). Understanding how animals use space in fragmented habitats is central to animal behavioral ecology and is key to determining the extent to which they can persist in an increasingly fragmented and human-dominated landscape (Fahrig 2007; Wilson *et al.* 2016).

Resources are often distributed unevenly in time and space across the landscape, which is exacerbated in fragmented environments (Fairgrieve 1995; Fahrig 2003). As a result, animals may modify their home range size and use in order to access sufficient resources (Law & Dickman 1998). Primates, in particular, have been shown to have considerable flexibility in their ranging patterns in response to fluctuations in resource availability (Clutton-Brock 1975; Di Bitetti 2001; Bartlett 2009). Furthermore, this relationship is more pronounced in frugivorous primates than in folivorous primates (Clutton-Brock 1977) due to the higher spatiotemporal fluctuations in fruit availability compared to leaves (Janson & Chapman 1999), and owing to the fact that fruit has a shorter digestion time than leaves (Demment & Laca 1991). The ability of a species to adapt to habitat fragmentation may therefore depend on their ability to exploit resources within suitable matrix habitat (Law & Dickman 1998; Fahrig 2007).

Studies exploring ranging patterns in small ranging species, such as primates, typically use ground-based phenology to determine the influence of resource availability (Di Bitetti 2001; Kaplin 2001; Twinomugisha & Chapman 2007; Albert *et al.* 2013; Gabriel 2013; Campera *et al.* 2014; Santhosh *et al.* 2015). Ground-based phenology provides detailed and accurate information on the availability of specific food items, yet often lacks spatial coverage (Studer *et al.* 2007). One of the most significant advances in ecological and conservation studies, however, has been the application of remotely sensed estimates of plant productivity, which has greatly enhanced our understanding of animal movement patterns (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Pettorelli *et al.* 2011; Neumann *et al.* 2015).

The Enhanced Vegetation Index (Huete *et al.* 2002) (EVI) is a remotely sensed correlate of photosynthetic activity and has consistently been used as an indicator of primary productivity (Paruelo *et al.* 1997), plant phenology (Justice *et al.* 1985) and canopy structure (Gamon *et al.* 1995). EVI represents the difference in earth surface reflectance patterns between the red and near-infrared parts of the electromagnetic spectrum, while taking into account the reflectance of the blue band (Eidenshink & Faundeen 1994). Values range from -1.0 (indicating non-vegetated areas) to $+1.0$ (densely vegetated areas) (Huete *et al.* 2002). Although remotely sensed estimates of plant productivity appear to have a complex relationship with ground-based estimates of food availability (Willems *et al.* 2009), the strong linear relationship with leaf cover has led to its application in ranging studies as an indirect measure of food availability, particularly in species which consume large proportions of leaves (Leimgruber *et al.* 2001; Ito *et al.* 2006; Willems *et al.* 2009; Villamuelas *et al.* 2016).

One of the main advantages of remotely sensed productivity over ground-based phenology, however, is the ability to monitor plant productivity over vast geographical scales and at regular time intervals (Huete *et al.* 2006; Lu *et al.* 2015). Because of this, the majority of studies applying remotely sensed productivity to animal ecology have been biased toward wide-ranging species (birds: Evans *et al.* 2006, carnivores: Nilsen *et al.* 2005, ungulates: Leimgruber *et al.* 2001; Ito *et al.* 2006). While the potential benefits of applying remotely sensed productivity to smaller-ranging species in fragmented habitats are vast, studies on primates, where there are pressing conservation concerns (Estrada *et al.* 2017), are almost entirely lacking (Zinner *et al.* 2002; Willems *et al.* 2009). However, remotely sensed productivity often lacks the spatial resolution and detail of ground-based phenology (Studer *et al.* 2007), meaning that regions sampled often include areas of lower productivity which may rarely be utilized or even inaccessible to forest-dwelling species (Lawes 1992). Despite this, the potential of remote sensing to identify areas of the habitat which are highest in plant productivity may provide valuable information on the ranging ecology of forest specialists capable of consuming large proportions of leaves. While each method of sampling phenology has its advantages, studies directly comparing their effectiveness are lacking (but see Gordo 2007; Willems *et al.* 2009; Villamuelas *et al.* 2016).

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The samango monkey (*Cercopithecus albogularis* subsp.: Dalton *et al*. 2015), a forest specialist, is threatened in South Africa (Linden *et al*. 2016). Their distribution is largely restricted to areas of tall-canopy, evergreen indigenous forests such as Afromontane/mistbelt, scarp, and coastal belt forests (Lawes 1990; Skinner & Chimimba 2005), which are becoming increasingly fragmented as a result of anthropogenic disturbance (Lawes 1992; Friedmann & Daly 2004; Kingdon *et al*. 2008). They are primarily arboreal and form single-male, multifemale groups (Henzi & Lawes 1987), averaging around 30 individuals (Lawes *et al*. 2013; Coleman & Hill 2014a). Unlike most other forest guenons, which are predominantly frugivorous (Lambert 2004), samango monkeys display considerable dietary flexibility and are able to consume large amounts of leaves (Coleman & Hill 2014a; Linden *et al*. 2015; Parker 2019). This is largely owing to their gut morphology and longer caecum (Bruorton & Perrin 1991), which facilitates the extraction of protein by breaking down cellulose in plant cell walls (Lawes *et al*. 1990; Bruorton & Perrin 1991; Lawes 1991). This dietary flexibility may account for the geographic range of the samango monkey extending to more southerly latitudes in comparison to other forest guenons (Wolfheim 1982; Coleman & Hill 2014a), and also facilitates the ranging of samangos into matrix habitat during periods of fruit scarcity (Lawes 1990; Skinner & Chimimba 2005; Nowak *et al*. 2017; Wimberger *et al*. 2017). Despite this, they are heavily reliant on food items located within patches of indigenous forest (Nowak *et al*. 2017; Wimberger *et al*. 2017) and are therefore reluctant to disperse over large stretches of open ground and inhabit small or isolated forest fragments (Lawes 1992, 2002; Lawes *et al*. 2000; Madisha *et al*. 2018). Understanding the factors that influence ranging patterns of the samango monkey is critical, therefore, for assessing the extent to which they can persist in an increasingly fragmented and human-dominated landscape.

The main aim of this study was to determine the influence of food availability (sampled locally), plant productivity (sampled remotely), and indigenous forest use on the monthly ranging patterns of the samango monkey. Secondly, in order to broaden the potential applicability of remotely sensed plant productivity to other small ranging guenons, we aimed to directly compare the effectiveness of each of these methods in explaining samango monkey ranging patterns. As the time available for ranging each day (Hill *et al*. 2003), and group size (Takasaki 1981), are both known to influence ranging patterns, we also collected data on this information to include as control variables in our analysis. Similarly, we included the number of days used to estimate monthly ranging patterns in our analysis to control for sample size (Getz *et al*. 2007). We predicted that the monthly ranging area, monthly core area and mean monthly daily path length of samango monkeys would increase during periods of low food availability and plant productivity, as resources become more spatially dispersed (Kaplin 2001; Boyle *et al*. 2009). We also predicted that monthly ranging patterns would increase when samango monkeys utilized less indigenous forest, as a result of monkeys ranging further into matrix habitat in order to access alternate food resources during periods of low productivity (Nowak *et al*. 2017; Wimberger *et al*. 2017). While remotely sensed plant productivity may provide an indirect measure of food availability in species which consume large proportions of leaves, we predicted that the phenological detail afforded by ground-based food availability would more accurately predict ranging patterns in a small ranging species.

MATERIALS AND METHODS

Study site

We conducted fieldwork at the Lajuma Research Centre in the western Soutpansberg Mountains, South Africa (23°02′23”S, 29°26′05”E) over a period of five years between February 2012 and December 2016. The isolated subpopulation of samango monkeys (*C. a. schwarzi*; Dalton *et al*. 2015) living on the mountain range is currently listed as Endangered (Linden *et al*. 2016), and represents the most vulnerable of the three samango monkey subspecies within South Africa (Linden *et al*. 2016). Across the mountain range there is substantial seasonal variation with cool, dry winters (mean seasonal temperature 16°C and mean seasonal total rainfall 16 mm) and hot, wet summers (mean seasonal temperature 20°C and mean seasonal total rainfall 561 mm), resulting in substantial variation in the spatial and temporal distribution of resources (Willems 2007). The south-facing cliffs also trap moisture resulting in fragmented patches of tall-canopy, evergreen indigenous mistbelt forest (Mucina & Rutherford 2006). These forests have extremely diverse plant communities, but prominent tall trees include lemonwood (*Xymalos monospora*), real yellowwood (*Podocarpus latifolius*), mountain wild-quince (*Cryptocarya transvaalensis*), forest waterberry (*Syzygium gerrardii*), and black ironwood (*Olea capensis* subsp. *macrocarpa*) (Mucina & Geldenhuys 2006). These forests are separated both naturally and anthropogenically by a mosaic of riparian forests, semi-deciduous woodlands, thicket, montane grasslands, farmland, and residential gardens, creating a

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diverse matrix habitat (Mostert *et al.* 2008). Altitude at the field site ranges from 1150 to 1750 m.

Data collection

We followed two well-habituated groups of samango monkeys; “Barn” (30–40 individuals) and “House” (60–70 individuals), for an average of nine complete days (max: 17, min: 2) every month across the study period. Complete days were defined as days where a group was followed from morning sleep site to evening sleep site, without losing audio-visual contact for more than 60 minutes (Coleman & Hill 2014b). Only months containing a minimum of five complete days were used in subsequent analyses, which appeared to be the minimum number of days which was representative of the areas visited by each group for that month (Seaman *et al.* 1999). This resulted in 97 “complete” months across the study period (Barn: 53, House: 44). During each full day we collected instantaneous scan samples (Altmann 1974), using a handheld PDA (Psion Teklogix Workabout Pro 3), on as many individuals as possible ($n = 36625$, mean: 6.2, max: 24, min: 1) within a five-minute window, at 20 minute intervals. General information collected during each scan sample included date, time and group ID, while we also recorded data on specific behaviors including feeding (chewing or ingesting food) and foraging (searching for food, picking/handling food) which were used to determine the diet preferences of the study groups. In addition, a GPS point (Garmin GPSmap 64S) of the group’s location was taken from the group’s centroid to coincide with the start of each scan sample, to within an accuracy of 5 m. This resulted in 113,373 locations for Barn group and 113,458 locations for House group.

Environmental monitoring in the field

We counted the number of leaves, fruit, and seed pods for 20 individually marked trees of 24 different species (480 trees in total) (Parker 2019) within the first two weeks of every month, over the five-year study period (Coleman & Hill 2014b). Trees were selected to give a representation of various habitat types, while also being considered important species in the samango monkey diet (Coleman 2013; Linden *et al.* 2015). Items were counted on an individually marked branch on each tree and then scaled up to give an estimate for each tree based on the estimated number of branches for that tree (Coleman & Hill 2014b). Where there were no items on the marked branch but items on the tree, either the total number of items were counted on the tree where possible, or estimates were made for the whole tree based on the number of items on another branch and the estimated number of branches for that tree (Coleman & Hill 2014b). In addition, we used randomly generated 5 m^2 vegetation plots across the study area ($n = 702$) to estimate the relative abundance of the 24 tree species monitored. Within each vegetation plot, all trees with a diameter at breast height >10 cm (Chapman *et al.* 1994; Clark & Clark 1999) were counted and identified where possible.

Remote sensing of the environment

We downloaded EVI composites for each month across the study period (2012–2016), at a resolution of 30 m^2, from the Landsat 7 & 8 databases from Google Earth Engine (https://earthengine.google.com). Images were downloaded for the entire western Soutpansberg Mountains. Monthly composites were used for comparability with the scale of ground-based food availability estimates. We used EVI in this analysis as it is more sensitive to changes in areas of high biomass, canopy differences, canopy structure, and plant phenology compared to other vegetation indices such as the Normalized Difference Vegetation Index (NDVI) (Huete *et al.* 2002), factors which are known to be important for space use in forest-dwelling species (Emerson *et al.* 2011; Coleman & Hill 2014b).

Estimation of ranging area and daily path length

To estimate the monthly ranging area of each group, we used adaptive localized convex hulls (*a*-LoCoH: Getz & Wilmers 2004; Getz *et al.* 2007), due to its superior ability of dealing with hard boundaries and its compatibility of coping with temporally close data points compared to other home range estimation methods (Getz & Wilmers 2004; Ryan *et al.* 2006; Getz *et al.* 2007). Ranging areas were created within the “*t*-LoCoH” package (Lyons *et al.* 2013) in R 3.4 (R Core Team 2017), using the maximum distance between monthly GPS points for each group as the *a*-value to allow correct construction of isopleths (Getz *et al.* 2007). We estimated two measures of ranging area (in hectares) for each group, for each month across the study period. Total monthly ranging area (monthly ranging area hereafter) was delineated by the 95% volume isopleth (Silverman 1986; Worton 1989; Getz *et al.* 2007), while monthly core ranging area (monthly core area hereafter) was delineated by the 50% volume isopleth (Börger *et al.* 2006; Getz *et al.* 2007). We defined ranging patterns in this way instead of more common terminology such as “home range” and “core home

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range," as a home range is typically determined over a yearly or multiyear period (Fleming *et al.* 2015). As such, monthly "home ranges" may not be representative of the actual home range. These ranging areas were then loaded into QGIS 2.18 (QGIS Development Team 2017) to extract estimates of plant productivity and indigenous forest use. Using the same method, we also estimated the overall home range size (overall home range hereafter) of each group using all GPS points collected across the study period, which was used to calculate estimates of food availability. Monthly mean daily path length (monthly DPL hereafter) was calculated by summing the straight-line distance (in km) between sequential GPS points from each scan sample across a complete day, using the distanceTrack function in the "argosfilter" package in R, and averaging across DPLs for each month.

Ground-based food availability estimates

We calculated monthly food availability estimates for leaves, fruit, and seed pods based on the five species for each food item which collectively contributed to over 60% of the samango monkey diet (Parker 2019). To do this, we averaged the number of leaves, fruit, and seed pods counted each month for each tree ($n = 20$) across each species ($n = 24$). This resulted in a monthly mean value per food item for each species across the study period. Flowers and other food items were excluded from analysis as they comprised such a small proportion of the diets of both groups across the study period (Table S1). We then scaled these values up to give representative values across the overall home range of each group. To do this, we multiplied these values by the estimated number of trees of each species (derived from the vegetation plots) within each group's overall home range, thus giving a representative monthly food availability estimate per food item (leaves, fruit and seed pods) for each of the 24 species sampled. The estimated number of trees within each group's range was calculated by dividing the area of each group's overall home range by the area of a vegetation plot (5 m^2), and then multiplying this figure by the mean number of trees per species across all plots ($n = 702$). To determine the five species which contributed over 60% of the samango monkey diet for each food item respectively, we summed the total number of scans recorded feeding and foraging on each food item of a particular species and then calculated this as a proportion of the total number of scans recorded feeding and foraging over the study period. Finally, we summed the total monthly food availability estimates for the five most consumed species of each food item respectively, thus giving an estimate of the monthly availability of the most commonly eaten fruits, leaves and seed pods respectively. As only four species of seed were eaten with any regularity across the study period (contributing 98% of all seed species eaten), we only included four seed species in our seed availability estimates.

Remotely sensed plant productivity and indigenous forest use estimates

Monthly EVI composites where cloud cover did not impede the study area by $>30\%$ were used in all analyses. For months where cloud cover exceeded this threshold, we selected the clearest image from the 16-day EVI composites. Composites were loaded into QGIS and a mean EVI value across each group's monthly ranging area was calculated for each sample month using the "zonal statistics" plugin, thus giving an indirect estimate for mean leaf availability across each group's range. EVI was run with a zero, 1- and 2-month time lag in subsequent analyses to allow for any possible lag in leaf availability between that sampled remotely and that which was available on the ground (Willems *et al.* 2009). EVI values for months where data were missing completely were estimated by averaging the values between the previous and following month. While estimating missing values in this way does not account for other factors that predict variation in EVI (e.g. ecological or physical factors), only 11 out of 118 sample months were missing and, as such, estimated values are likely to be representative. As using mean plant productivity across the ranging area in this way may mask areas or periods of particularly high or low productivity, we also identified the areas of each group's monthly range which were highest in plant productivity. To do this, we clipped EVI rasters by values >0.5, a value which represents dense vegetation (Huete *et al.* 2006), within the monthly ranging area using the "Raster Calculator." We then calculated these areas as a proportion of each group's monthly ranging area using the "LecoS" (Landscape ecology Statistics) (Jung 2016) plugin in QGIS, for each month across the study period. Finally, to calculate the proportion of monthly ranging area that included indigenous forest, we used the "indigenous forest" layer of the 2014 SANBI (South African National Biodiversity Institute) landcover map (30 m^2 resolution) and calculated this as a proportion of each group's monthly ranging area using the "LecoS" (Jung 2016) plugin in QGIS. The SANBI indigenous forest layer is derived from a combination of seasonal maximum NDVI values (from images taken between April 2013 and April 2014), forest biome boundaries (from the SANBI database), and shadow and altitude terrain parameters (from NASA's Shuttle Radar Topography Mission database).

Data analysis

We used linear mixed-effects models with a Gaussian error structure to determine the effects of food availability, plant productivity, and indigenous forest use on the ranging patterns of samango monkeys. For each of the home range variables (monthly ranging area, monthly core area, and mean monthly daily path length), we used separate models to determine the effect of ground-based food availability, remotely sensed plant productivity, and proportion of indigenous forest and areas of high plant productivity incorporated into the monthly ranging area. We ran separate models in this way due to collinearity between multiple variables (Bolker *et al.* 2008), while also allowing for comparison in explanatory power between methods. We included day length, group size, and number of "complete" days used to estimate monthly ranging patterns as control variables, while month and year were included as random variables. Models were fitted in R 3.4 (R Core Team 2017) using the lmer function of the "lme4" package (Bates *et al.* 2014). We checked for normality and homogeneity of residuals by visually inspecting histograms and qqplots of the residuals, and the residuals plotted against fitted values. Collinearity between fixed effects were inspected using Variance Inflation Factors (VIF) from the vif function within the "car" package. VIF values were derived from a standard linear model excluding the random effects, with all values <1.5 indicating no collinearity between variables (Hair *et al.* 2014). *P*-values for the individual effects were based on likelihood ratio tests comparing the full model with respective reduced models, dropping one fixed effect at a time (R function drop1), with significance inferred at the 5% level. To allow for likelihood ratio tests we fitted the models using Maximum Likelihood (Bolker *et al.* 2008) and used Akaike's Information Criterion (Burnham & Anderson 2002) to infer goodness of fit between separate models.

Ethical statement

All behavioral data collection followed the Association for the Study of Animal Behavior (ASAB) Guidelines for the Treatment of Animals in Behavioral Research and Teaching (ASAB 2012) and were covered by the Liverpool John Moores University's use of Live Animals in Unregulated Research Protocol (NK_EP/2016-10). All fieldwork was approved by the Life Sciences Ethical Review Process Committee and the Department of Anthropology Ethics Committee at Durham University, UK and was conducted with approved permits from Limpopo Province Department of Economic Development and Tourism (LEDET).

RESULTS

Overall home range size across the study period was considerably larger for House (123.9 ha) group compared to Barn (89.7 ha), with home ranges between the groups overlapping significantly (Fig. 1). Visualization of the home ranges also highlights a clear avoidance of large open areas, cliff faces, and hard boundaries, with the core areas focused within the indigenous forest. While monthly ranging area varied considerably within each group, ranges were fairly consistent between groups (Barn group max: 52.0 ha, min: 11.4 ha; House group max: 58.1 ha, min: 14.3 ha).

We found no effect of ground-based food availability (Table 1) or remotely sensed plant productivity (Table 2) on the monthly ranging area, monthly core area, or mean monthly DPL. This also held when introducing a 1- and 2-month time lag into the analysis to account for possible delays in remotely sensed plant productivity (Table S2). We found that both monthly ranging area and mean monthly DPL significantly decreased as more areas of high plant productivity were included within the monthly ranging area, but found no effect on the monthly core area (Table 3). Similarly, we found that both monthly ranging area and monthly core area significantly decreased as more indigenous forest was incorporated into the monthly ranging area (Fig. 2, Table 4). However, the proportion of monthly ranging area comprising indigenous forest was not related to mean monthly DPL. The proportion of indigenous forest within the monthly ranging area was also positively correlated with areas of high plant productivity (likelihood ratio test: $t = 4.20$, df = 1, $P < 0.001$).

Proportion of monthly ranging area containing indigenous forest best explained variation in monthly ranging patterns compared to ground-based food availability and remotely sensed plant productivity, based on log likelihood ratio tests and model information criterion. In addition, proportion of areas of high plant productivity within the monthly ranging area was a better predictor of total monthly ranging area and mean monthly DPL than food availability or plant productivity sampled across the ranging area (Table 5).

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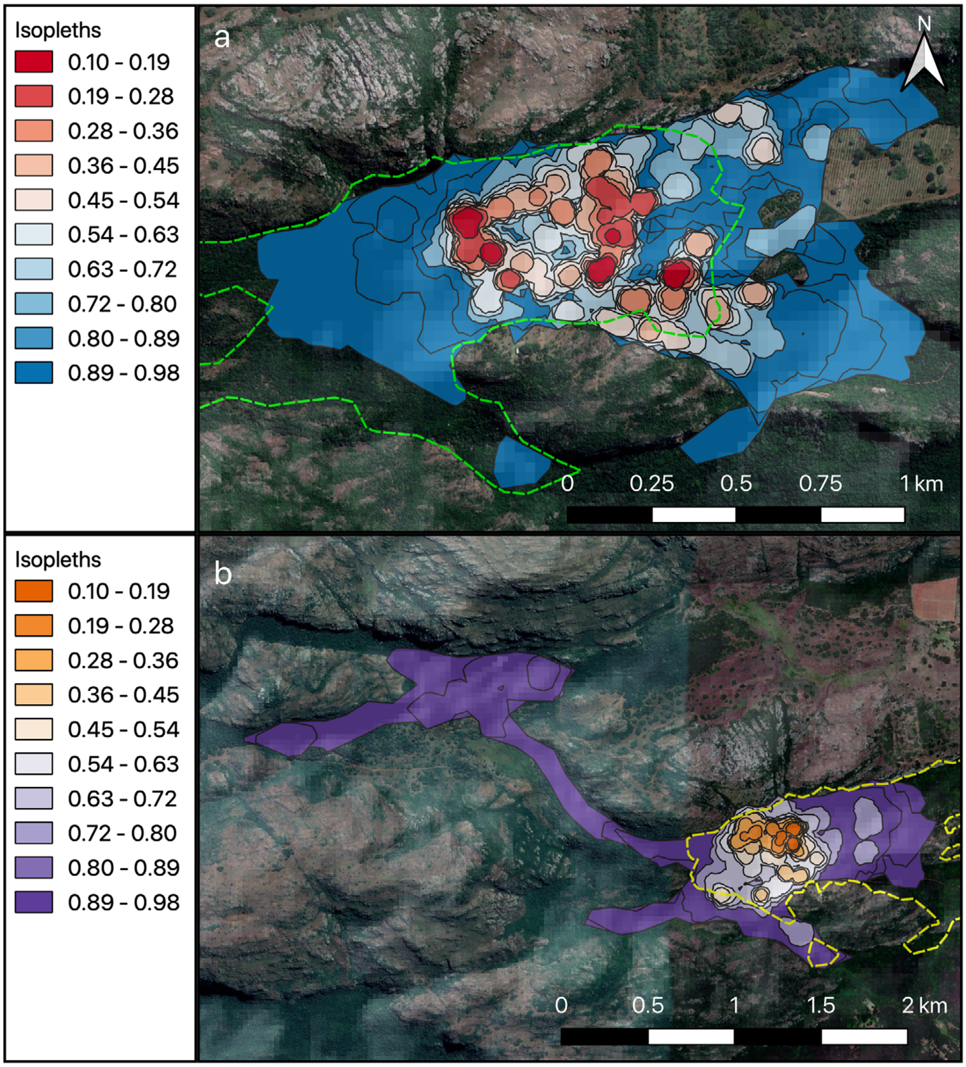

Figure 1 Utilization distributions (UDs) showing the overall home range size and location for both (a) Barn and (b) House groups in the Soutpansberg Mountains, South Africa, across the study period (2012–2016). Outline of House group's (green dotted line, image a) and Barn group's (yellow dotted line, image b) home range are shown to highlight the proximity of each group in relation to each other and to indicate that home ranges overlapped. Total home range is delineated as isopleths ≤ 0.98. Core home range is delineated as isopleths ≤ 0.5.

DISCUSSION

Understanding the influence of resource availability on space use is central to assessing the adaptability of a species to habitat fragmentation (Fahrig 2007; Wilson *et al*. 2016). Here, we explored the influence of food availability, plant productivity, and indigenous forest use on the monthly ranging patterns of the endangered samango monkey in the Soutpansberg Mountains, South Africa. While we found no effect of ground-based food availability or remotely sensed plant productivity sampled across the ranging area on monthly ranging patterns, we found that utilization of both areas high in plant productivity and indigenous forest were significantly associated with a reduction in some aspects of monthly ranging.

Both total and core monthly ranging area significantly decreased as more indigenous forest was incorporated into the ranging area, suggesting that by utilizing more of this habitat type samango monkeys can increasingly focus their ranges on this highly productive habitat. Reliance on natural forest fragments is commonly observed in frugivorous species, such as bats (Ripperger *et al*. 2015) and

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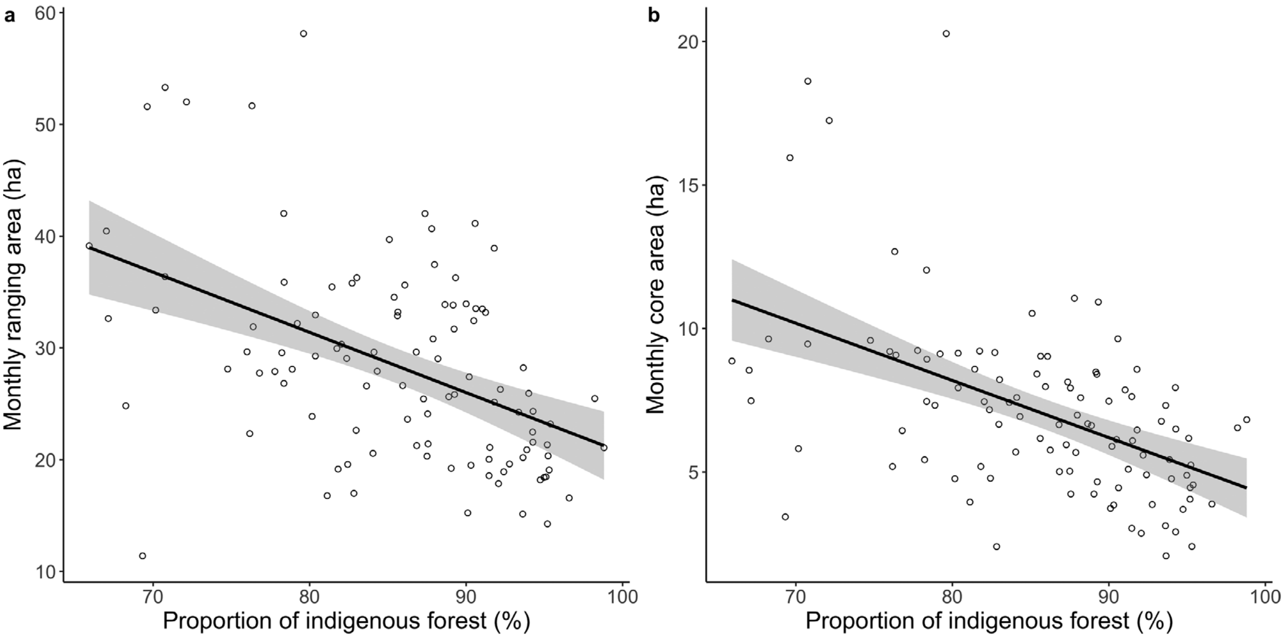

Figure 2 Effect of proportion of monthly ranging area including indigenous forest on (a) size of monthly ranging area and (b) monthly core area.

primates (Estrada & Coates-Estrada 1996; Nowak *et al.* 2017), which typically reduce their ranging area by incorporating more natural forest fragments into the home range (Chaverri *et al.* 2007; Palminteri & Peres 2012; Campera *et al.* 2014). Similarly, our results demonstrate the importance of the indigenous forest as a highly productive habitat to samango monkeys and that in order to live at reasonable population densities, access to indigenous forest patches is key for this species (Linden *et al.* 2016; Nowak *et al.* 2017). The indigenous forest contains important indigenous fruits, such as figs (Linden *et al.* 2015), which contribute significantly to the samango monkey diet (Coleman 2013; Linden *et al.* 2015; Parker 2019). For example, samango monkeys in the Eastern Cape preferentially forage on indigenous fruits and seeds when available regardless of the availability of exotic species which provide a higher calorific content (Nowak *et al.* 2017; Wimberger *et al.* 2017). Similarly, while samangos at Lajuma are capable of utilizing matrix habitat to access alternate resources during periods of low productivity, access to these natural forest fragments is clearly key (Wimberger *et al.* 2017). By incorporating more indigenous forest into the ranging area, samangos are able to reduce their ranging and access more preferred food items in the indigenous forest (Coleman 2013; Linden *et al.* 2015), thereby reducing the need to exploit the habitat matrix as intensively.

In contrast, mean monthly DPL was not influenced by indigenous forest use. While indigenous forest may be important for daily ranging patterns in terms of connectivity between forest patches (Swart & Lawes 1996), the daily distance travelled appears to be more influenced by the time available for foraging (indicated by day length) in this study (Hill *et al.* 2003). However, other factors such as weather (Isbell 1983; Hill 1999), intergroup encounters (Yamagiwa & Mwanza 1994), predator avoidance (Willems & Hill 2009; Coleman & Hill 2014b), mating season dynamics (Erlinge *et al.* 1990), and sleep site location (Albert *et al.* 2011) may also be important. Furthermore, daily path length may not be a reliable measure when exploring ranging patterns in samango monkeys, as their reluctance to traverse open ground (Lawes 1992, 2002; Lawes *et al.* 2000) may superficially increase travel paths when going around, rather than through, open areas.

We also found that as samango monkeys incorporated more areas of high plant productivity into the ranging area, both the total monthly ranging area and mean monthly DPL significantly decreased. These areas represent the most densely vegetated parts of the ranging area (Huete *et al.* 2002) which are highest in plant biomass (Paruelo *et al.* 1997; Willems *et al.* 2009). Therefore, while these areas may include important fruit species (Nowak *et al.* 2017; Wimberger *et al.* 2017), the ability

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Table 1 Coefficient estimates and key statistics of models predicting effect of availability of leaves, fruit, and seed pods on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
Ranging area						
Intercept	0.291	0.153	−0.024	0.623	(1)	(1)
Leaves	−0.011	0.011	−0.034	0.012	−1.023	0.329
Fruit	−0.005	0.007	−0.020	0.010	−0.673	0.502
Seed pods	−0.005	0.008	−0.022	0.012	−0.603	0.554
Day length	−0.007	0.013	−0.034	0.019	−0.572	0.568
Days	**0.007**	0.002	0.002	0.012	2.840	0.006
Group	0.003	0.015	−0.026	0.032	0.183	0.857
Core area						
Intercept	0.124	0.051	0.020	0.237	(1)	(1)
Leaves	−0.007	0.004	−0.015	0.001	−1.758	0.103
Fruit	0.001	0.003	−0.005	0.007	0.336	0.738
Seed pods	−0.004	0.003	−0.010	0.003	−1.153	0.271
Day length	−0.005	0.004	−0.014	0.003	−1.266	0.213
Days	0.001	0.001	−0.001	0.003	0.815	0.431
Group	0.003	0.006	−0.009	0.014	0.491	0.630
DPL						
Intercept	−0.365	0.251	−0.861	0.130	(1)	(1)
Leaves	−0.016	0.023	−0.061	0.029	−0.705	0.483
Fruit	−0.023	0.019	−0.061	0.015	−1.217	0.225
Seed pods	−0.013	0.021	−0.056	0.029	−0.626	0.535
Day length	**0.150**	0.020	0.110	0.190	7.464	<0.001
Days	0.007	0.007	−0.007	0.021	1.033	0.321
Group	0.012	0.037	−0.062	0.086	0.316	0.753

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. (1) not shown because of having no meaningful interpretation.

Table 2 Coefficient estimates and key statistics of models predicting effect of mean plant productivity across the ranging area on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
Ranging area						
Intercept	0.387	0.155	0.062	0.719	(1)	(1)
Productivity	0.057	0.059	−0.062	0.177	0.958	0.346
Day length	−0.018	0.013	−0.047	0.010	−1.346	0.187
Days	**0.008**	0.002	0.003	0.013	3.410	0.001
Group	−0.005	0.013	−0.031	0.021	−0.385	0.701
Core area						
Intercept	0.166	(1)	0.054	0.054	(1)	(1)
Productivity	0.015	0.406	0.023	−0.031	0.061	0.524
Day length	−0.009	3.648	0.005	−0.020	0.000	0.056
Days	0.001	1.128	0.001	−0.001	0.003	0.288
Group	−0.001	0.016	0.005	−0.011	0.010	0.900
DPL						
Intercept	−0.294	0.231	−0.750	0.163	(1)	(1)
Productivity	−0.085	0.133	−0.351	0.184	−0.636	0.532
Day length	**0.148**	0.021	0.105	0.190	6.960	<0.001
Days	0.007	0.007	−0.006	0.021	1.125	0.284
Group	−0.007	0.034	−0.075	0.061	−0.208	0.836

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Productivity, mean plant productivity (indexed by enhanced vegetation index) sampled across the total monthly ranging area. (1) not shown because of having no meaningful interpretation.

of samangos to incorporate a large proportion of leaves in their diet (Coleman & Hill 2014a; Parker 2019) may serve to reduce some aspects of ranging patterns by utilizing more areas which are high in plant productivity. The lack of relationship observed with the monthly core area is likely a result of the consistency in the spatial and temporal availability and distribution of high plant productivity areas within the core range, in addition to the location of important resources such as sufficient sleeping trees (Kaplin 2001). We also found that the proportion of areas high in plant productivity and indigenous forest within the ranging area were positively correlated, indicating that the most productive areas of the landscape are disproportionately found within this habitat type.

In contrast, neither ground-based food availability nor remotely sensed plant productivity sampled across the ranging area influenced samango monkey ranging patterns, which contradicted our predictions. However, this is perhaps unsurprising given our previous findings, in that by utilizing more areas high in plant productivity, which are disproportionately located within the indigenous forest, samangos can reduce aspects of ranging patterns owing to their dietary flexibility (Coleman & Hill 2014a; Linden *et al*. 2015; Wimberger *et al*. 2017) (Table S1). By focusing ranging on these areas, samangos can access sufficient resources either by consuming indigenous fruits when available, or by increasing consumption of leaves, which are readily available and easily located (Hemingway & Bynum 2005), when fruit is

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Table 3 Coefficient estimates and key statistics of models predicting effect of proportion of areas of high plant productivity within the ranging area on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
Ranging area						
Intercept	0.320	0.131	0.044	0.600	(1)	(1)
High productivity	**−0.006**	0.003	−0.011	−0.001	−2.309	0.029
Day length	−0.005	0.011	−0.029	0.018	−0.451	0.652
Days	**0.007**	0.002	0.002	0.011	2.815	0.006
Group	−0.005	0.013	−0.031	0.021	−0.400	0.690
Core area						
Intercept	0.151	0.047	0.051	0.256	(1)	(1)
High productivity	−0.001	0.001	−0.003	0.001	−1.086	0.323
Day length	−0.007	0.004	−0.016	0.002	−1.636	0.110
Days	0.001	0.001	−0.001	0.003	0.826	0.419
Group	−0.001	0.005	−0.011	0.010	−0.121	0.904
DPL						
Intercept	−0.321	0.219	−0.754	0.112	(1)	(1)
High productivity	**−0.013**	0.006	−0.024	−0.001	−2.156	0.033
Day length	**0.157**	0.019	0.119	0.194	8.300	<0.001
Days	0.005	0.007	−0.008	0.019	0.821	0.429
Group	−0.005	0.034	−0.071	0.062	−0.135	0.893

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. High productivity, proportion of areas of high plant productivity within the total monthly ranging area. (1) not shown because of having no meaningful interpretation.

Table 4 Coefficient estimates and key statistics of models predicting effect of proportion of ranging area containing indigenous forest on total monthly ranging area, core ranging area, and daily path length

Variable	Estimate	SE	CI_{lower}	CI_{upper}	*t*-value	*P*
Ranging area						
Intercept	0.564	0.141	0.264	0.854	(1)	(1)
Forest use	**−0.004**	0.001	−0.006	−0.002	−4.237	<0.001
Day length	−0.004	0.011	−0.027	0.019	−0.357	0.722
Days	**0.007**	0.002	0.003	0.012	3.413	0.001
Group	0.008	0.013	−0.016	0.034	0.677	0.502
Core area						
Intercept	0.248	0.047	0.149	0.344	(1)	(1)
Forest use	**−0.002**	0.000	−0.002	−0.001	−4.780	<0.001
Day length	−0.004	0.004	−0.012	0.003	−1.178	0.248
Days	0.001	0.001	−0.001	0.002	0.984	0.335
Group	0.005	0.005	−0.004	0.015	1.101	0.277
DPL						
Intercept	−0.038	0.256	−0.545	0.468	(1)	(1)
Forest use	−0.004	0.002	−0.009	0.001	−1.618	0.110
Day length	**0.149**	0.018	0.113	0.186	8.124	<0.001
Days	0.009	0.006	−0.004	0.022	1.369	0.192
Group	0.008	0.035	−0.062	0.077	0.218	0.828

Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Forest use, proportion of monthly ranging area containing indigenous forest. (1) not shown because of having no meaningful interpretation.

scarce. The ability to utilize a range of resources in these areas may reduce the need to exploit the habitat matrix as intensively, thereby masking any influence of food availability and plant productivity across the ranging area. Similarly, plant productivity sampled across the ranging area was also uninformative. This was likely a consequence of the arboreal nature of samango monkeys, which are reluctant to disperse over large stretches of open ground or non-forested habitat (Lawes 1992, 2002; Lawes *et al.* 2000), areas which would have influenced this productivity estimate. Interestingly, Willems *et al.* (2009) also found no correlation between NDVI (another remotely sensed estimate of plant productivity) and either home range or core home range size in vervet monkeys (*Chlorocebus pygerythrus*) at the same field site, but found a negative association with DPL. However, unlike samangos, vervets are not predominantly forest-dwelling (Willems *et al.* 2009) and so daily ranging patterns may be suitably explained by productivity across the home range as vervets are more capable of utilizing open habitats which are largely avoided by samangos (Lawes 2002). Although plant productivity across the ranging area was uninformative, our findings demonstrate the capacity of remote sensing to identify areas of the habitat which are highest in plant productivity, and that these areas appear much more informative when exploring ranging patterns in small ranging, forest-dwelling guenons.

Contrary to our predictions, we found that the proportion of indigenous forest within the monthly ranging area best explained monthly ranging patterns, based on log likelihood ratio tests and model information criterion. While ground-based estimates of food availability

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Table 5 Candidate model set and model selection results for total ranging area, core ranging area, and daily path length

Ranging variable	Model	Fixed effects	LogLik	ΔLogLik	AIC	ΔAIC$_c$	*w*
Ranging area	4	Forest use + Day length + Days + Group	133.3	7.8	−250.5	0.0	1.00
	3	High productivity+ Day length + Days + Group	127.5	2.0	−238.9	11.6	0.00
	1	Productivity + Day length + Days + Group	125.5	0.0	−235.1	15.4	0.00
	2	Leaves + Fruit + Seeds + Day length + Days + Group	125.9	0.4	−231.8	18.7	0.00
Core area	4	Forest use + Day length + Days + Group	236.3	9.9	−456.5	0.0	1.00
	3	High productivity + Day length + Days + Group	226.7	0.3	−437.4	19.1	0.00
	1	Productivity + Day length + Days + Group	226.4	0.0	−436.9	19.6	0.00
	2	Leaves + Fruit + Seeds + Day length + Days + Group	227.7	1.3	−435.5	21.0	0.00
Daily path length	3	High productivity + Day length + Days + Group	31.3	1.5	−46.6	0.0	0.24
	4	Forest use + Day length + Days + Group	30.3	0.5	−44.6	2.0	0.08
	1	Productivity + Day length + Days + Group	29.2	−0.6	−42.4	4.2	0.03
	2	Leaves + Fruit + Seeds + Day length + Days + Group	30.1	0.3	−40.3	6.3	0.02

ΔLogLik, difference in log likelihood compared to the best model; AIC$_c$, Akaike information criterion corrected for small sample size; ΔAIC$_c$, difference in AIC$_c$ compared to the best model; *w*, Akaike weight. Ranging area, total monthly ranging area; core area, monthly core area; DPL, mean monthly daily path length. Forest use, proportion of monthly ranging area containing indigenous forest; High productivity, proportion of areas of high plant productivity within the total monthly ranging area; Productivity, mean plant productivity (indexed by enhanced vegetation index) sampled across the total monthly ranging area.

offer greater phenological detail, the dietary flexibility and reliance of samangos on the indigenous forest ultimately determines the variation in monthly ranging patterns. Conversely, when focusing their range less on these areas, samangos can exploit alternate resources in the surrounding matrix habitat. This flexibility may help to mitigate the effects of habitat loss and fragmentation by facilitating movement between forest fragments. However, access to indigenous forest is clearly key to samango monkey ranging patterns (Nowak *et al*. 2017). In order for samango monkeys to persist in an increasingly fragmented and human-dominated landscape, proper management of these forests is essential (Swart & Lawes 1996). Across South Africa, metapopulations are declining owing to increasing habitat loss and a lack of corridors connecting suitable habitats (Lawes 2002). This is particularly relevant for the subpopulations in the Soutpansberg Mountains which are isolated from neighboring populations (Linden *et al*. 2016). Management plans should therefore focus on expanding protected areas of indigenous forest through reclaiming and restoring non-viable areas (Linden *et al*. 2016). In addition, minimizing disturbance in and around large forest patches (Lawes *et al*. 2000) and continuing to connect forest fragments is also crucial in order to facilitate movement between patches and ensure the long-term viability of subpopulations (Swart & Lawes 1996).

The results from our study highlight the potential of using remote sensing to identify areas of the habitat which are particularly high in plant productivity, and demonstrate the applicability of using this measure to explore ranging patterns in a small ranging, forest-dwelling guenon. The ability of samango monkeys to utilize a range of food items within these areas, which are predominantly located within the indigenous forest, appears key to explaining monthly ranging patterns. Therefore, effective management of these forests is essential in order to ensure the long-term persistence of the samango monkey in an increasingly fragmented and human-dominated landscape.

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REFERENCES

Albert A, Savini T, Huynen M (2011). Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology* **12**, 1–9.

Albert A, Huynen MC, Savini T, Hambuckers A (2013). Influence of food resources on the ranging pattern of Northern pig-tailed macaques (*Macaca leonina*). *International Journal of Primatology* **34**, 696–13.

Altmann J (1974). Observational study of behavior: Sampling methods. *Behaviour* **49**, 227–67.

ASAB (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* **83**, 301–9.

Bartlett TQ (2009). *The Gibbons of Khao Yai: Seasonal Variation in Behavior and Ecology*. Routledge, Abingdon.

Bates D, Mächler M, Bolker B, Walker S (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **1**, 883–5.

Bolker BM, Brooks ME, Clark CJ *et al*. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24**, 127–35.

Börger L, Franconi N, De Michele G *et al*. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* **75**, 1393–405.

Boyle SA, Lourenço WC, da Silva LR, Smith AT (2009). Travel and spatial patterns change when *Chiropotes satanas chiropotes* inhabit forest fragments. *International Journal of Primatology* **30**, 515–31.

Bruorton M, Perrin M (1991). Comparative gut morphometrics of vervet (*Cercopithecus aethiops*) and samango (*C. mitis erythrarchus*) monkeys. *International Journal of Mammalian Biology* **56**, 65–71.

Burnham KP, Anderson DR (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Campera M, Serra V, Balestri M *et al*. (2014). Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology* **35**, 957–75.

Chapman CA, Wrangham RW, Chapman LJ (1994). Indicies of habitat-wide fruit abundance in tropical forest. *Biotropica* **26**, 160–71.

Chaverri G, Quiros OE, Kunz TH (2007). Ecological correlates of range size in the tent-making bat *Artibeus watsoni*. *Journal of Mammalogy* **88**, 477–86.

Clark DA, Clark DB (1999). Assesing the growth of tropical rain forest trees: Issues for forest modeling and management. *Ecological Applications* **9**, 981–97.

Clutton-Brock TH (1975). Ranging behavior of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Animal Behaviour* **23**, 706–22.

Clutton-Brock TH (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Clutton-Brock TH, ed. *Primate Ecology*. Academic Press, London, UK, pp. 539–56.

Coleman BT (2013). *Spatial and temporal determinants of samango monkey (*Cercopithecus mitis erythrarchus*) resource acquisition and predation avoidance behaviour*. Durham University, Durham.

Coleman BT, Hill RA (2014a). Biogeographic variation in the diet and behaviour of *Cercopithecus mitis*. *Folia Primatologica* **85**, 319–34.

Coleman BT, Hill RA (2014b). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour* **88**, 165–73.

Dalton DL, Linden B, Wimberger K *et al.* (2015). New insights into samango monkey speciation in South Africa. *PLoS ONE* **10**, e0117003.

Demment MW, Laca EA (1991). Herbivory: the dilemma of foraging in a spatially heterogenous food environment. In: Palo RT, Robbins CT, eds. *Plant Defenses Against Mammalian Herbivory*. CRC Press, Boca Raton, FL, pp. 29–44.

Di Bitetti MS (2001). Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *The Zoological Society of London* **253**, 33–45.

Eidenshink JC, Faundeen JL (1994). The 1 km AVHRR global land data set: First stages in implementation. *International Journal of Remote Sensing* **15**, 3443–62.

Emerson SE, Brown JS, Linden JD (2011). Identifying Sykes' monkeys', *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Animal Behaviour* **81**, 455–62.

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Erlinge S, Hoogenboom I, Agrell J, Nelson J, Sandell M (1990). Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. *Journal of Mammalogy* **71**, 597–3.

Estrada A, Coates-Estrada R (1996). Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology* **17**, 759–83.

Estrada A, Garber PA, Rylands AB *et al.* (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances* **3**, 1–16.

Evans KL, James NA, Gaston KJ (2006). Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography* **15**, 372–85.

Fahrig L (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* **34**, 487–15.

Fahrig L (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology* **21**, 1003–15.

Fairgrieve C (1995). *The comparative ecology of blue monkeys* (Cercopithecus mitis stuhlmannii) *in logged and unlogged forest, Budongo Forest Reserve, Uganda: the effects of logging on habitat and population density*. University of Edinburgh, Edinburgh, UK.

Fischer J, Lindenmayer D (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**, 265–80.

Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* **96**, 1182–8.

Friedmann Y, Daly B (2004). *Red data book of the mammals of South Africa: A conservation assessment*. Conservation Breeding Specialist Group (SSC/IUCN), Southern Africa, Endangered Wildlife Trust, South Africa.

Gabriel DN (2013). Habitat use and activity patterns as an indication of fragment quality in a strepsirrhine primate. *International Journal of Primatology* **34**, 388–6.

Gamon JA, Field CB, Goulden ML *et al.* (1995). Relationships between NDVI, canopy structure, and photosynthesis in three californian vegetation types. *Ecological Applications* **5**, 28–41.

Getz WM, Wilmers CC (2004). A local nearest neighbor convex-hull construction of home ranges and utilization distribution. *Ecography* **27**, 489–5.

Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* **2**, e207

Gordo O (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* **35**, 37–58.

Haddad NM, Brudvig LA, Clobert J *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Applied Ecology* **1**, e1500052.

Hair JJ, Black W, Babin B, Anderson R (2014). *Multivariate Data Analysis*, 7th edn. Pearson Education, Harlow, UK.

Hemingway CA, Bynum N (2005). The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP, eds. *Seasonality in primates*. Cambridge University Press, Cambridge, UK, pp. 57–4.

Henzi SP, Lawes MJ (1987). Breeding season influxes and the behaviour of adult male samango monkeys (*Cercopithecus mitis albogularis*). *Folia Primatologica* **48**, 125–36.

Hill RA (1999). *Ecological and demographic determinants of time budgets in baboons: implications for cross-populational models of baboon socioecology*. University of Liverpool, Liverpool, UK.

Hill RA, Barrett L, Gaynor D *et al.* (2003). Day length, latitude and behavioural (in)flexibility in Baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* **53**, 278–86.

Huete AR, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* **83**, 195–13.

Huete AR, Didan K, Shimabukuro YE *et al.* (2006). Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters* **33** (6), 2–5.

Isbell LA (1983). Daily ranging behavior of Red Colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. *Folia Primatologica* **41**, 34–48.

Ito TY, Miura N, Lhagvasuren B *et al.* (2006). Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *Journal of Zoology* **269**, 291–8.

Janson CH, Chapman CA (1999). Resources and primate community structure. In: Fleagle JG, Janson CH, Reed KE, eds. *Primate Communities*. Cambridge University Press, Cambridge, UK, pp. 237–61.

Jung M (2016). LecoS: A python plugin for automated landscape ecology analysis. *Ecological Informatics* **31**, 18–21.

Justice CO, Townshend JRG, Holben BN *et al.* (1985). Analysis of the phenology of global vegetation using meteorological satellite data. *International Journal of Remote Sensing* **6**, 1271–318.

Kaplin BA (2001). Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology* **22**, 521–48.

Kerr JT, Ostrovsky M (2003). From space to species: Ecological applications for remote sensing. *Trends in Ecology and Evolution* **18**, 299–5.

Kingdon J, Gippoliti S, Butynski TM *et al.* (2008). *Cercopithecus mitis. IUCN Red List of Threatened Species*. [Cited 29 Sep 2018]. Available from www.iucnredlist.com

Lambert JE (2004). Resource switching and species coexistence in guenons: A community analysis of dietary flexibility. In: Glenn ME, Cords M, eds. *The Guenons: Diversity and Adaptation in African Monkeys*. Springer, Boston, MA, pp. 309–23.

Law BS, Dickman CR (1998). The use of habitat mosaics by terrestrial vertebrate fauna: Implications for conservation and management. *Biodiversity and Conservation* **7**, 323–33.

Lawes MJ (1990). The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. *Journal of Biogeography* **17**, 669–80.

Lawes MJ (1991). Diet of samango monkeys (*Cercopithecus mitis erythrarchus*) in the Cape Vidal Dune Forest, South Africa. *Journal of Zoology* **224**, 149–73.

Lawes MJ (1992). Estimates of population density and correlates of the status of the samango monkey *Cercopithecus mitis* in Natal, South Africa. *Biological Conservation* **60**, 197–10.

Lawes MJ (2002). Conservation of fragmented populations of *Cercopithecus mitis* in South Africa: the role of reintroduction, corridors and metapopulation ecology. In: Glenn ME, Cords M, eds. *The Guenons: Diversity and Adaptation in African Monkeys*. Academic/Plenum Publishers, New York, pp. 375–92.

Lawes MJ, Henzi SP, Perrin MR (1990). Diet and feeding behaviour of samango monkeys (*Cercopithecus mitis labiatus*) in Ngoye forest, South Africa. *Folia Primatologica* **54**, 57–69.

Lawes MJ, Mealin PE, Piper SE (2000). Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. *Conservation Biology* **14**, 1088–98.

Lawes MJ, Cords M, Lehn C (2013). *Cercopithecus mitis* profile. In: Kingdon J, Kalina J, eds. *The Mammals of Africa: Vol II. Primates of Africa*. University of California Press, Berkeley, CA, pp. 354–62.

Leimgruber P, McShea WJ, Brookes CJ, Bolor-Erdene L, Wemmer C, Larson C (2001). Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia. *Biological Conservation* **102**, 205–12.

Linden B, Linden J, Fischer F, Linsenmair KE (2015). Seed dispersal by South Africa's only forest-dwelling guenon, the samango monkey (*Cercopithecus mitis*). *African Journal of Wildlife Research* **45**, 88–99.

Linden B, Wimberger K, Ehlers-Smith Y, Child MF (2016). A conservation assessment of *Cercopithecus albogularis*. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, eds. *The Red List Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, Midrand, South Africa, pp. 1–12.

Lindenmayer DB, Fischer J (2006). *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, DC.

Lu L, Kuenzer C, Wang C, Guo H, Li Q (2015). Evaluation of three MODIS-derived vegetation index time series for dryland vegetation dynamics monitoring. *Remote Sensing* **7**, 7597–614.

Lyons AJ, Turner WC, Getz WM (2013). Home range plus: A space-time characterization of movement over real landscapes. *Movement Ecology* **1** (2), 1–14.

Madisha MT, Dalton DL, Jansen R, Kotze A (2018). Genetic assessment of an isolated endemic samango monkey (*Cercopithecus albogularis labiatus*) population in the Amathole Mountains, Eastern Cape Province, South Africa. *Primates* **59**, 197–7.

Mostert THC, Bredenkamp GJ, Verwey C, Mostert RE, Hahn N (2008). Major vegetation types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa. *African Protected Area Conservation and Science* **50**, 32–48.

Mucina L, Geldenhuys C (2006). Afrotemperate, subtropical and azonal forests. In: Mucina L, Geldenhuys C, eds. *The Vegetation of South Africa, Lesotho and*

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Swaziland. South African National Biodiversity Institute, Pretoria, South Africa, pp. 585–14.

Neumann W, Martinuzzi S, Estes AB *et al*. (2015). Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Movement Ecology* **3**, 8.

Nilsen EB, Herfindal I, Linnell JDC (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience* **12**, 68–75.

Nowak K, Hill RA, Wimberger K, le Roux A (2017). Risk-taking in samango monkeys in relation to humans at two sites in South Africa. *Ethnoprimatology* **1**, 301–14.

Palminteri S, Peres CA (2012). Habitat selection and use of space by bald-faced sakis (*Pithecia irrorata*) in Southwestern Amazonia: Lessons from a multiyear, multigroup study. *International Journal of Primatology* **33**, 401–17.

Parker EJ (2019). *Ranging Patterns and Resource Use in Samango Monkeys*. Liverpool John Moores University, Liverpool.

Paruelo JM, Epstein HE, Lauenroth WK, Burke IC (1997). ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* **78**, 953–8.

Pettorelli N, Ryan S, Mueller T *et al*. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research* **46**, 15–27.

QGIS Development Team (2017). *Quantum GIS*. Open Source Geospatial Foundation Project, Chicago, IL.

R Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ripperger SP, Kalko EKV, Rodríguez-herrera B (2015). Frugivorous bats maintain functional habitat connectivity in agricultural landscapes but rely strongly on natural forest fragments. *PLoS ONE* **10**, e0120535.

Ryan SJ, Knechtel UC, Getz W (2006). Range and habitat selection of African buffalo in South Africa. *The Journal of Wildlife Management* **70**, 746–76.

Santhosh K, Kumara HN, Velankar AD, Sinha A (2015). Ranging behavior and resource use by lion-tailed macaques (*Macaca silenus*) in selectively logged forests. *International Journal of Primatology* **36**, 288–10.

Saunders DA, Hobbs RJ, Margules CR (1991). Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* **5**, 18–32.

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management* **63**, 739–47.

Silverman BW (1986). *Density Estimation for Statistics and Data Analysis*. Chapman & Hall, London, UK.

Skinner JD, Chimimba CT (2005). *The Mammals of the Southern African Sub-region*. Cambridge University Press, Cambridge, UK.

Studer S, Stöckli R, Appenzeller C, Vidale PL (2007). A comparative study of satellite and ground-based phenology. *International Journal of Biometerology* **51**, 405–14.

Swart J, Lawes MJ (1996). The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. *Ecological Modelling* **93**, 57–74.

Takasaki H (1981). Troop size, habitat quality, and home range area in Japanese macaques. *Behavioral Ecology and Sociobiology* **9**, 277–81.

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M (2003). Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* **18**, 306–14.

Twinomugisha D, Chapman CA (2007). Golden monkey ranging in relation to spatial and temporal variation in food availability. *African Journal of Ecology* **46**, 585–93.

Villamuelas M, Fernández N, Albanell E *et al.* (2016). The Enhanced Vegetation Index (EVI) as a proxy for diet quality and composition in a mountain ungulate. *Ecological Indicators* **61**, 658–66.

Willems EP (2007). From space to species: Integrating remotely sensed information on primary productivity into investigations and systems models of vervet monkey *(Cercopithecus aethiops) socio-ecology*. Durham University, Durham.

Willems EP, Barton RA, Hill RA (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology* **20**, 985–92.

Willems EP, Hill RA (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology* **90**, 546–55.

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Wilson MC, Chen XY, Corlett RT *et al*. (2016). Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecology* **31**, 219–27.

Wimberger K, Nowak K, Hill RA (2017). Reliance on exotic plants by two groups of threatened samango monkeys, *Cercopithecus albogularis labiatus*, at their southern range limit. *International Journal of Primatology. International Journal of Primatology* **38**, 151–71.

Wolfheim JH (1982). *Primates of the World: Distribution, Abundance and Conservation*. University of Washington Press, Seattle, WA.

Worton ABJ (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–68.

Yamagiwa J, Mwanza N (1994). Day-journey length and daily diet of solitary male gorillas in lowland and highland habitats. *International Journal of Primatology* **15**, 207–24.

Zinner D, Fernando P, Torkler F (2002). Distribution and habitat of grivet monkeys (*Cercopithecus aethiops aethiops*) in eastern and central Eritea. *African Journal of Ecology* **40**, 151–8.

SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Monthly range and average time spent feeding (%) on different food items by each samango monkey group at Lajuma between 2012 2016. Average values from Coleman & Hill, 2014 (also collected from Barn group) also shown to demonstrate values are characteristic of the groups.

Table S2 Coefficient estimates and key statistics of models predicting effect of mean plant productivity across the ranging area, with a one and two-month lag, on total monthly ranging area.

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Reactive and pre-emptive spatial cohesion in a social primate

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Spatial cohesion in group-living animals is assumed as a risk-sensitive characteristic. Few studies have explicitly investigated this assumption or asked whether risk-related changes in spatial cohesion operate over short-term or long-term scales. We explored whether two groups of wild samango monkeys, *Cercopithecus albogularis schwarzi*, would adjust cohesion in reaction to naturally occurring risk from eagles and intergroup encounters using the number of conspecific neighbours as our response. Data on these directly observed encounters were used to assess reactive responses to immediate events. GPS-recorded locations of these encounters allowed us to create relative risk landscapes to investigate whether these groups might pre-emptively increase cohesion in high risk locations, in the absence of a direct threat. Multimodel inference was used to compare support for candidate models representing biological hypotheses. We found support for changes in cohesion in reaction to immediate intergroup conflict in both study groups. In contrast, only eagle risk apparently elicited a pre-emptive response. These results suggest that spatial cohesion is risk sensitive, but that responses differ between types of risk and between groups.

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Spatial cohesion in animal social groups refers to the extent to which members maintain interindividual proximity. This type of cohesion is important for the stability of groups (Trillmich, Fichtel, & Kappeler, 2004). Individuals benefit from cohesion through greater protection from predators, due to safety in numbers (Bertram, 1978; Elgar, 1989; Zhao, Lyu, Sun, & Zhou, 2019), and enhanced access to social information about potential risks or resources (Evans, Votier, & Dall, 2016; Fernández-Juricic & Kacelnik, 2004). While animals can reactively adjust their behaviour to the immediate environment, they can also make decisions based on information gathered from previous experience and memory (Bracis & Mueller, 2017; Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Dröge et al., 2019). This prior information might also lead animal groups to pre-emptively alter their spacing where they perceive greater risk. In this study we address the question of whether a wild social primate – the samango monkey, *Cercopithecus albogularis schwarzi* – might flexibly adjust spatial cohesion in response to both immediate risks (reactive increase) and pre-emptively in response to variation in risk perception across the landscape.

PREDATION AND SPATIAL COHESION

Social prey species often perceive themselves to be under greater risk when they have fewer conspecific neighbours nearby (e.g. Fernández-Juricic, Beauchamp, & Bastain, 2007), and numbers of immediate neighbours may be a more important determinant of individual risk perception than absolute group size (Treves, 1998). There is also evidence that cohesion itself is sensitive to variation in perceived risk. Chivers, Brown, and Smith (1995) used experiments with predator chemical cues on groups of fathead minnows, *Pimephales promelas*, and found that the groups became tightly cohesive postexposure. Similarly, observations of hamandryas baboons, *Papio hamadryas*, indicated that groups maintained closer spatial cohesion on mornings after a group had encountered a night predator (Schreier & Swedell, 2012). Domestic sheep, *Ovis aries*,

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have also been found to reactively aggregate when targeted by trained dogs (King et al., 2012).

Behavioural responses to risk can operate over both short-term scales in response to immediate danger and over long-term scales, such as with landscape-level variation in predation risk (Dröge et al., 2019). Even in the absence of a direct threat, experience with risky habitat types or locations might elicit pre-emptive responses based on prior knowledge (Fagan, 2013). The ability to perceive these differences in safety allows prey species to shift their behavioural strategies or space use accordingly (Arias-Del Razo, Hernández, Laundré, & Velasco-Vázquez, 2012; Laundré, Hernández, & Altendorf, 2001; Willems & Hill, 2009). Pre-emptive responses can reduce the probability that individuals or groups will encounter a predator and be forced to react to an immediate threat. For example, smaller groups of wild bison, *Bison bison*, selected safer habitats compared to when the same individuals formed larger groups (Fortin et al., 2009). Yet, whether social animals alter within-group spatial cohesion in response to locations where they have had prior encounters with predators or other dangers is uncertain.

Previous research at our study site indicates that risk from eagles is an important determinant of samango landscape utilization (Coleman & Hill, 2014a). Moreover, observers recorded predatory encounters between these species relatively frequently (L. R. LaBarge, personal observation). Research on this study population also indicates that humans modulate samango risk perception from terrestrial carnivores (Nowak, le Roux, Richards, Scheijen, & Hill, 2014). Thus, this study is focused on the more commonly encountered eagle predators.

INTERGROUP COMPETITION

Collective intergroup defence has been observed across a variety of group-living species including social carnivores, birds and primates (Heinsohn & Packer, 1995; Müller & Manser, 2007; Radford, Majolo, & Aureli, 2016). Such conflict can be risky (Radford et al., 2016; Shopland, 1982), and evidence suggests that maintaining spatial cohesion with other group members may be important for effective defence and individual safety. For example, male West African chimpanzees, *Pan troglodytes verus*, in the Tai Forest remain relatively cohesive even while foraging in separate parties, presumably because intergroup conflicts may require collective action (Eckhardt, Polansky, & Boesch, 2015). Upon detecting the scents of other groups, banded mongoose, *Mungos mungo*, produce calls that result in recruitment of fellow group members, and direct encounters often include collective aggression (Müller & Manser, 2007). Following aggressive intergroup encounters, cohesion may also be high when many individuals engage in affiliative behaviours as a result of stress/anxiety (Radford et al., 2016) or ongoing perceptions of conflict risk. If an animal or group behaves pre-emptively towards landscape/habitat-level variation in perceived predation risk, then it may follow that perceived risk of intergroup competition may also result in similar responses. Previous studies that have focused on competition between sympatric carnivore species have found evidence that smaller species avoid locations where they might encounter larger competitors (Berger & Gese, 2007; Broekhuis et al., 2013). However, we found fewer examples of prey species exhibiting similar shifts with regards to intraspecies conflict (but see Benadi, Fichtel, & Kappeler, 2008). Yet, if groups need to maintain cohesion to collectively defend against competitors, then we might expect individuals to pre-emptively seek proximity to their group members in areas of heightened risk. Doing so could provide greater safety, enhance individuals' abilities to engage in conflict and/or facilitate information transfer for early warning about potential threats.

Samango intergroup encounters typically involve aggression from only adult females (Henzi, Payne, & Lawes, 2003; Lawes & Henzi, 1995). One report described female group members attacking and killing a dispersing female (Payne, Lawes, & Henzi, 2003), but other studies report that few conflicts result in physical aggression (Henzi, et al., 2003). Prior research on our samango monkey population found that study groups tended to avoid areas of high eagle risk, but not areas of high intergroup encounter risk (Coleman & Hill, 2014a). One possible explanation for this is that prey species that are already constrained by the need to avoid predation might use other pre-emptive strategies to mitigate this additional risk. Additionally, groups may not preferentially avoid areas where intergroup conflict is high because they may be resource rich (Brown, 2013), and engaging in competition may maintain ranging area and outweigh the potential costs.

ADDITIONAL SOCIAL AND ECOLOGICAL VARIABLES

In this study we focus on whether spatial cohesion in a social primate might be risk sensitive and whether these responses are reactive and/or pre-emptive. To investigate these questions, additional variables need to be accounted for that could also plausibly influence spatial cohesion. Among these are variation in the number of group members engaged in social behaviours that necessarily require proximity, variation in the immediate availability of food sources and local habitat characteristics. For example, greater amounts of within-group competition should result in disaggregation (Heesen, Macdonald, Ostner, & Schülke, 2015). Conversely, higher rates of affiliative social behaviours should result in short-term increases in cohesion (Sugiura, Shimooka, & Tsuji, 2011).

The effect of the immediate availability of high-quality, spatially clustered food items on spatial cohesion might also be mediated by a species' tendency towards high or low levels of intragroup feeding competition. Heesen et al. (2015) observed that wild Assamese macaques, *Macaca assamensis*, were less cohesive while feeding, while hamandryas baboon bands were more likely to break into one-male units when foraging in habitats with lower food availability (Schreier & Swedell, 2012). Both observations were potentially due to animals foraging away from group members to avoid contest competition. Other species may aggregate more closely while foraging, because individuals might take advantage of social information to locate food items (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), or because a patchy distribution of food across the environment facilitates clustering within a small area. Red-tailed monkeys, *Cercopithecus ascanius*, (Bryer, Chapman, & Rothman, 2013), patas monkeys, *Erythrocebus patas*, and vervets, *Chlorocebus pygerythrus* (Isbell & Enstam, 2002), all tend to forage more closely to conspecifics when feeding on fruits, which are rarer and more spatially clumped than leaves or insects. Here we account for variation in social and foraging behaviour by the inclusion of control variables in all our models to better estimate the effects of risk.

Characteristics of individual groups, including group size and demographics, may be important predictors of typical levels of cohesion. While beyond the scope of this study, it is important to note that as group size increases, feeding competition may also increase in many primate species (Janson, 1988; Janson & Goldsmith, 1995), leading to differently sized groups varying in cohesion. Additionally, larger groups may be more likely to attack a competing group and 'push' competitors away (Furrer, Kyabulima, Willems, Cant, & Manser, 2011; Wilson, Kahlenberg, Wells, & Wrangham, 2012), although this is not always the case (Crofoot, Gilby, Wikelski, & Kays, 2008). Thus, different groups will likely differ in how they respond to environmental variation. Here we use data on two relatively large groups and therefore cannot investigate this, but we account for potential effects of group identity throughout our analysis.

Habitat characteristics such as visibility should limit the ability of individuals to monitor others (Fernández-Juricic et al., 2007). Low visibility may lead individuals to seek proximity to groupmates, increasing their overall cohesion, or, conversely, losing track of neighbours and becoming disaggregated. Visibility is also often related to the likelihood of detecting an approaching or hiding predator (Fortin et al., 2009). Previous research on our population of samangos indicated that this population avoids areas of low understory visibility, independently of variation in the spatial distribution of resources (Coleman & Hill, 2014a). Canopy cover may, however, impact perception differently in this species, because areas where vertical visibility is high could be riskier for monkeys because they may be more easily targeted by aerial predators (Shultz, 2001), although some cover should be necessary for an eagle to ambush monkeys from within the canopy (Shultz, Noë, McGraw, & Dunbar, 2004).

PRESENT STUDY

We used handheld global positioning systems (GPS) data and direct behavioural observation of samango monkeys collected over 17 months in the Afromontane forests of northern South Africa to examine potential associations between spatial cohesion and risk at two different temporal scales. Our response and proxy for spatial cohesion was the number of conspecific neighbours counted within scan samples. Specifically, we hypothesized the following.

(1) Samangos would exhibit reactionary changes in cohesion to immediate risk. We predicted that groups would become more cohesive while threatened by competitors or predators.

(2) Samangos would pre-emptively alter spatial cohesion in response to location-specific risk in the absence of any direct threat. Thus, we predicted that cohesion might change along with variation in location-specific risk, rendering reactionary responses to threats unnecessary.

To investigate these hypotheses, we compared sets of plausible candidate models (Table 1) (Burnham, Anderson, & Huyvaert, 2011) while controlling for variation in the immediate availability of relatively rare food sources, habitat characteristics, group identity and potential variation in within-group social behaviour. We then use top models to further investigate these predictions.

METHODS

Study Site and Species

We conducted our study at the Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo, South Africa (23°02′S, 29°26′E) using long-term data collected by the Primate and Predator Project. The study site encompasses an array of habitat types including tall moist Afromontane forest, deciduous woodland, acacia bush and rocky grassland/cliffsides. We studied two samango groups, ‘Barn’ (*N* ~ 35) and ‘House’ (*N* ~ 70–80), that were well habituated to direct observation. Samangos are medium-sized (adult females ~ 4.4 kg, adult males ~7.6 kg), arboreal, mainly frugivorous monkeys that live in single-male multifemale groups typically with 10–65 individuals (Coleman & Hill, 2014a). Natural predators of samangos at this site include crowned eagles, *Stephanoaetus coronatus*, and black eagles, *Aquila verreauxii*, the African leopard, *Panthera pardis* (Grey, Bell, & Hill, 2017), caracal, *Caracal caracal* (Nowak et al., 2014), and, potentially, rock pythons, *Python sebae*. While samangos at this site face risk from multiple predators, we focus on predation from raptors in this study because previous research has shown them to be the primary driver of space use in this environment (Coleman & Hill, 2014a). We do not distinguish between eagle species in our analysis.

Ethical Note

We received research permission from the Limpopo Province Dept of Economic Development and Tourism (Permit No. ZA/LP/81996). This research was also approved by the Institutional Animal Care and Use Committee of the University at Buffalo (IACUC No. ANT07037N) and the Durham University Animal Welfare Ethical Review Board. All project members and research assistants collecting direct behavioural data on these habituated groups received training and protocols to maintain human/animal safety through

Table 1
Candidate models and their components

Hypothesis	Model	Response	Offset	Fixed effects	Random effects
Null	0	Count of nearest neighbours	No. of individuals per scan sample	**Control variables**: Samango group ID; habitat structure (canopy cover, understory visibility); proportion feeding rare/spatially clumped fruiting trees; within-group aggression and affiliative behaviour	Time of sample × Unique 'event' ID × Spatial location
Hypothesis 1 (reactive changes only)	1	"	"	Null + Risky 'events'	"
Hypothesis 1 (reactive changes interacted with habitat structure)	2	"	"	Null + Risky 'events' × Habitat structure	"
Hypothesis 1 + 2 (combined reactive + pre-emptive changes)	3	"	"	Null + Risky 'events' + Relative eagle risk + Relative intergroup risk (location-specific)	"
Hypothesis 2 (pre-emptive changes only)	4	"	"	Null + Relative eagle risk + Relative intergroup encounter risk	"
Hypothesis 2 (eagle risk only)	5	"	"	Null + Relative eagle risk	"
Hypothesis 2 (intergroup encounter risk only)	6	"	"	Null + Relative intergroup encounter risk	"
Hypothesis 2 (eagle risk interacted with habitat structure)	7	"	"	Null + Relative eagle risk × Habitat structure	"
Hypothesis 2 (intergroup risk interacted with habitat structure)	8	"	"	Null + Relative intergroup risk × Habitat structure	"

Response is modelled with an offset to correct for variation in the number of individuals per scan sample.

the Primate and Predator Project. Observers were trained to observe animals with binoculars from a distance, avoid direct eye contact and any other potentially disturbing behaviours to minimize observer bias and potential stress to animals.

Behavioural Data Collection

Behavioural and location data were collected from August 2016 until December 2017. We collected data on each study group from dawn to dusk, 3–4 days a week via scan sampling (Altmann, 1974); the behaviour of as many individuals as possible within the group was recorded during a 5 min window every 20 min throughout the day. Study days ranged from a minimum of 10.5 h (0640–1720 h) in the austral winter to a maximum of 14.5 h in the summer (0440–1900 h). Most individuals within both groups were not individually recognizable. We minimized the possibility of repeating samples on the same individual within a 5 min scan by moving throughout the group and collecting data only when we were certain we had not previously recorded an individual. Within scans, we recorded the time, date, group ('House' or 'Barn'), individual age–sex class and individual identity when an individual was known. We used five general behavioural categories of 'feeding', 'resting', 'socializing', 'moving' or 'other' and recorded more specific categories within each of these. When an individual was feeding, we attempted to identify the plant or insect species and recorded the type of food item taken. When two or more individuals were grooming one another, we only sampled one individual (the first one an observer saw). Additionally, we recorded the number of noninfant neighbours each individual samango had within 5 m as a proxy for group cohesion. This included neighbours within 5 m that were above or below the sampled individual. This method follows Treves (1999) on the closely related blue monkey, *Cercopithecus mitis*. As the number of individuals sampled varied between 5 min scan windows, we accounted for this in our analysis (see Statistical Analysis). The distance of 5 m was chosen as a balance between collecting neighbour data and remaining accurate through low-visibility habitats. We minimized bias and attempted to obtain data representative of the whole group by moving positions with each subsampled individual from the centre to the periphery and sampling between subgroups. This should have given us a relatively realistic picture of overall group spatial cohesion during a 5 min sample, regardless of absolute group size.

Along with each scan sample, we collected a GPS point with a handheld device (Garmin GPSmap 60Cx or 62s, Garmin, Olathe, KS, U.S.A.) prior to behavioural data collection. We recorded the location and details of all predator encounters, intergroup encounters, alarm vocalizations and within-group aggression ad libitum. In this data set, we included eagle predation attempts and encounters that elicited alarm vocalizations from group members, but we excluded observations of large birds flying overhead if subjects did not react. Responses to intergroup conflict ranged from alarm vocalizations to direct aggression and chasing. For most of these encounters there was no obvious 'winner' of the conflict. We later noted whether an encounter had occurred during or within 5 min of the beginning of a scan sample window. Encounters occurring outside this time may have less of an effect on behaviour and therefore we excluded these data (and subsequent 20, 40 and 60 min scans).

Nineteen observers (including L.R.L and A.T.L.A.) collected behavioural data. Training in data collection, including identification of food plant species, lasted approximately 3–5 weeks. Assistants were trained by A.T.L.A. to navigate between the periphery and centre of (sub)groups confidently within and between scan samples. This was to ensure that as much of the group was sampled as possible consistently throughout the day. Regular testing and monitoring by A.T.L.A. ensured that assistants did not follow single smaller subgroups for the duration of observation days and scan windows. At the end of this period each trainee was observed by A.T.L.A. over the course of a full follow day or until several hours of consecutive instantaneous scans were in complete agreement to ensure interobserver reliability. Trainees collected data independently only after successfully completing this assessment and were then subject to checks by A.T.L.A. to ensure consistency.

Vegetation and Habitat Data

We collected vegetation data in 25 m^2 quadrant randomly distributed across the home ranges of the two samango groups to measure habitat visibility and canopy cover, and to collect information on the size and distribution of fruiting tree species following Brower, Zar, and von Ende (1998), Coleman and Hill (2014a), and Willems and Hill (2009). Coleman and Hill (2014a) found that visibility measured in similarly designed 5 × 5 m plots was a significant predictor of landscape use in this samango population, indicating that these methods measure variables on a scale relevant for this species. In each plot, we measured horizontal habitat visibility in each cardinal direction at 5 m and 10 m from each plot corner using photographs of a 1 × 1 m chequerboard with 225 squares. The percentage of the board that was visible was averaged across these photographs for one measure of horizontal visibility. Canopy cover was measured through photographs taken directly upward through a 1 × 1 m square held parallel to the ground. We then used ImageJ (Rueden et al., 2017; National Institutes of Health, Bethesda, MD, U.S.A.) to calculate the number of dark pixels to estimate the percentage of the photo that was foliage as a proxy for canopy cover. To obtain location-specific values for horizontal visibility and canopy cover, we created rasters using location and attribute data from 905 vegetation plots distributed randomly across the home range of each group using the open-source software RStudio 3.5.0 (R Core Team, 2018) and the packages 'raster' (Hijmans et al., 2017) and 'sp' (Pebesma, 2018) with a resolution of 25 m. For those cells that contained more than one point, we obtained the mean of the attribute values. We used location data collected alongside behavioural scan samples to extract attribute data based on the nearest grid cell (Supplementary Figs S1–S6). Thus, for every scan sample location, we obtained a value for canopy cover and understory visibility.

We also collected data on all trees within each vegetation plot that we identified as mature individuals (>10 cm circumference at breast height) and listed the species when possible. Any trees that were located on the boundary rope of the plot were sampled if any part of the main stem/trunk was within the plot. Previous studies (e.g. Coleman & Hill, 2014b) and scan-sampled data allowed us to identify food plant species important for samango monkeys at this site. Of these food species, we further identified which produced fruits and had large crown diameters that could potentially support a large proportion of a foraging samango group (mean crown of ≥10 m). From this information we then ranked these trees by relative abundance and identified the 10 rarest species that could support co-feeding as *Ficus burkei, Ficus craterostoma, Ficus sur, Ekebergia capensis, Acacia sieberiana, Trychillia dregeana, Rauvolfia caffra, Syzygium cordatum, Croton sylvaticus* and *Celtis africana.* Behavioural scan data on the number of individuals feeding on these species was then used to calculate the proportion of a sample feeding on these relatively rare and large fruiting trees and this variable was included as a control in all models.

Relative Risk Data

We created maps for the relative risk of intergroup encounters and eagle encounters for every month of the study period to assess whether groups might pre-emptively increase cohesion in risky areas. We created kernel density estimates (KDEs) of each type of risk per each group based on GPS recorded locations of eagle encounters and intergroup encounters. The values for risk for each observation were based on the previous 12 months of data collection, with these data from August 2015. Therefore, events that happened later than an observation, but during the same month, were not included. We created these density estimates with the *R* package adehabitat (Calenge, 2006) and used plug-in bandwidth selection, which performs well for small sample sizes (Gitzen, Millspaugh, & Kernohan, 2006). We created kernel density estimated utilization distributions (UDs) using GPS data collected

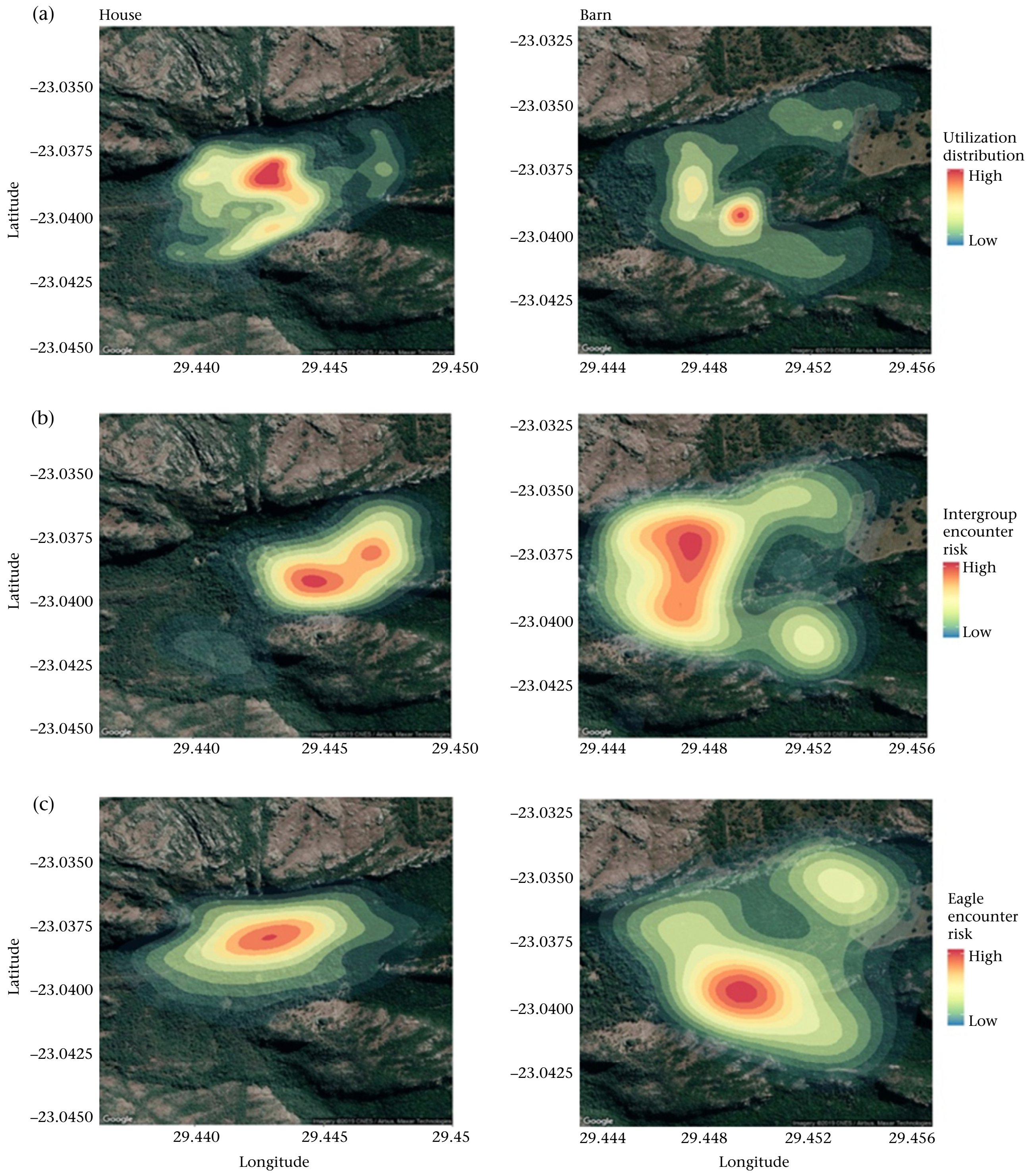

Figure 1. (a) Utilization distribution (100%) for the two groups based on frequency of GPS points recorded prior to all scan samples collected for the 12 months preceding each sample. (b) Eagle risk for the two groups based on frequency of encounters ($N = 67$ for Barn and $N = 61$ for House) that were used to create relative risk values based on kernel density estimation. (c) Intergroup encounter risk. Colours represent relative values ($N = 205$ for Barn and $N = 92$ for House). Rasters created for calculating relative risk were updated monthly with points from the previous 12 months and were converted to UTM and corrected for overall utilization.

during scan samples. These were similarly created from the previous 12 months for each month of observations. In total, we created 17 KDEs of eagle encounters and 17 KDEs of intergroup encounters for each group to be paired with the same number of UDs. We then converted density estimates to rasters and divided each month's eagle encounter and intergroup encounter density estimate by its UD to obtain monthly risk values for both types of threat relative to how frequently locations were used (Fig. 1). This method corrects for how often we observed samangos in a particular location to ensure that areas visited more frequently were not erroneously weighed as being riskier than more rarely visited areas. We used these location-specific risk values as predictors for perceived eagle risk and perceived intergroup encounter risk to assess whether groups might pre-emptively change their cohesion in the absence of a direct threat following Willems and Hill (2009) and Coleman and Hill (2014a). Importantly, these relative risk maps represent where samangos might be more likely to perceive themselves as being at risk of encountering an eagle or competing group due to previous experience while under observation. We do not assume this method creates a landscape of intrinsic risk that is consistently true for when groups are unobserved by a human. As previous studies on this species have found that perception of risk of terrestrial predators is modulated by a 'human-shield,' their overall landscape of risk is likely somewhat different when not in the presence of researchers (see Discussion).

Statistical Analysis

Our analysis focused on behavioural samples collected in the hour preceding and following 144 intergroup encounters and 74 eagle encounters and predation attempts. Our response variable was the total count of nearest neighbours across all individuals included within a 5 min scan window. We offset the response by the number of individuals that we collected data on during a sample in all our models to account for this variation. When an offset is added to the equation, the rate is modelled, allowing the response to vary with the exposure (number of samangos sampled in a scan window) (Brooks et al., 2017). We restricted scan samples to those in which data were collected on five or more individuals for a total of 1129 scan samples clustered within 218 events.

Our predictor for reactionary changes in cohesion to immediate risks was a categorical variable that denoted whether a behavioural sample occurred in the absence of either of these events (baseline), during (within 5 min) of an intergroup encounter (IGE) or eagle encounter (EE), or whether the sample was collected 20, 40 or 60 min following these events. The duration of eagle encounters tended to be short, and thus occurred within one behavioural sample, whereas conflicts between groups often lasted through two or more samples. If an intergroup or eagle encounter occurred outside of a scan sample window (or within 5 min of a sample), then we excluded that data. Scan sample locations (UTM) were used to extract eagle and intergroup encounter relative risk values for each line of data.

We compared several candidate models for group spatial cohesion using an information-theoretic framework to conduct multimodel inference. We preferred this approach to null-hypothesis testing because Akaike weights provide a quantitative measure of empirical support for each alternative model, given the observed data. This procedure is also appropriate given that our hypotheses were nonmutually exclusive and that the procedure works for both nested and non-nested models (Burnham et al., 2011). We used the small-sample corrected Akaike information criteria (AICc) as this criterion works well for a range of sample sizes. Our null model assumed that risk variables were not good predictors of cohesion but included habitat and behavioural variables likely to be important. Our other models included at least one pre-emptive or reactionary risk variable so we could compare support between the models as well as between the models and the null. For a list of predictors included in each candidate model see Table 1.

Our response variable was overdispersed, therefore we fitted the data to Poisson mixed effects models with a random effect for each scan sample using a unique ID to account for this moderate amount of variance past the mean (Harrison, 2014) using the *R* package GLMM Template Model Builder (glmmTMB) (Brooks et al., 2017). In all models, the random effects of the time of the scan sample were crossed with a unique ID for each event (one of the 218 clusters). We further checked assumptions and simulated residuals for spatial and temporal autocorrelation in a maximal model using the package DHARMa (Hartig, 2017). While we did not detect significant spatial autocorrelation, we included a spatial random effect within all models to account for nonindependence between points located closely together (based on Euclidean distance, Brooks et al., 2017). Because we used models with a log link, our response offset is included as the natural log of the number of individuals we sampled within a scan. All models included the fixed effects of 'group' to account for potential variation due to group identity. We further included the number of within-group aggressive encounters that occurred up to the time of each scan sample and the proportion of individuals engaged in affiliative social behaviour (play, grooming) at the time of a sample in all models as control variables.

Habitat visibility measures (understory, canopy) and the proportion of sampled individuals feeding on rare fruiting trees were also included in all models to account for these potential effects. However, because habitat attributes might affect predation risk in this species (Coleman & Hill, 2014a), we included this variable as an interaction term in certain models because location-specific risk perception may depend on habitat structure as well as previous experience. Finally, our predictor for feeding/foraging behaviour was the proportion of individuals within a behavioural scan sample feeding on fruits of the large and rare species identified from vegetation plots. This predictor was chosen rather than quantifying the absolute amount of food in a given patch because short-term changes in group-level feeding behaviour could affect overall cohesion (e.g. Bryer et al., 2013; Isbell & Enstam, 2002). Our reasoning for this choice was that resource availability may not necessarily influence cohesion when individuals are engaged in nonfeeding activities.

We considered the 'best' models to have the highest model weights and lower ΔAICc (Δ_i) values (Anderson & Burnham, 2004; Richards, Whittingham, & Stephens, 2011) and present parameter estimates of these top models. Commonly used practice considers $\Delta_i < 2$ to be practically equivalent and models with $\Delta_i < 6$ not discounted (Anderson & Burnham, 2004; Richards, 2005). Many do not recommend to model averaging coefficients of discrete distributions or models with random structures (Cade, 2015). However, estimates of fixed effects we present here show only small differences and no change in sign/direction, which also renders model averaging predictions unnecessary (Bolker et al., 2009). We do not present *P* values for these coefficients for assessing parameter importance as much evidence indicates these values may not be reliable for inference in final models (Brewer, Butler, & Cooksley, 2016; Freedman & Freedman, 1983). Furthermore, these values do not necessarily translate to biological significance (Burnham et al., 2011). We assess trends with variables of interest using model predictions (and their 95% prediction intervals) and marginal effects while holding other variables at their mean or reference values for improved inference (for model summaries including *P* values, see Supplementary Table S3). This allowed us to investigate our reactionary versus pre-emptive questions separately by removing reactionary effects to look at potential pre-emptive changes between high-risk and low-risk locations in the absence of a direct encounter. We calculated and plotted values transformed back to counts of nearest neighbours using the 'ggeffects' package to visualize the influence of each variable on the response (Lüdecke, 2018). Random effect variance was set to zero for calculating population-level values. Additionally, we used the package 'sjstats' (Lüdecke, 2018) to calculate interclass correlation coefficients (ICC) for the random structure of our models. Finally, we calculated the marginal and conditional pseudo-R^2 of each model following Nakagawa and Schielzeth (2013) to provide information about the explanatory ability of each model.

RESULTS

Our data set included 1129 scan samples clustered into 218 events (144 intergroup encounters and 74 eagle encounters). Two of our candidate models fit our criteria as potentially being the 'best' fitting model of the set. These were model 1 representing reactionary changes to eagle or intergroup encounters and model 3 combining reactionary changes and pre-emptive changes with no interactions (Table 2). This initial selection provides evidence that both reactionary and pre-emptive responses to risk may occur. Estimates for parameters found in both models were similar in magnitude and direction (Supplementary Table S3). Our control variables for within-group behaviour (aggression and affiliative social behaviour) both appeared to be predictors of increased cohesion (Supplementary Figs S1 and S2) and were thus important to account for. Additionally, we noted a small positive association between feeding on relatively rare fruiting trees and cohesion (Supplementary Fig. S3), but estimates for this variable were close to zero and the prediction intervals were wide. Finally, neither understory visibility nor canopy cover appeared to be strongly associated with our measure of group spatial cohesion.

ICC values for random effects indicated that the time of day the scan sample occurred did not explain any variance (0.0) in the response, whereas the proportion explained by 'event ID' was 0.254 and the proportion explained by geographical location was 0.213. These results indicate that cohesion was relatively consistent within the same day and between instances when groups returned to the location of a raster cell. Marginal pseudo-R^2 values, which approximate the variance explained by the fixed effects, indicate that our candidate models explained 12.86–15.03% of the variation in cohesion. Conditional values indicate that combined fixed and random effects explained 52.73–55.12% of the variation in cohesion (Table 2).

Hypothesis 1: Samangos Exhibit Reactionary Changes in Cohesion to Immediate Risk

During baseline observations, the Barn group tended to be more cohesive, with ~10 neighbours per scan sample, versus the House group, with ~7 neighbours (Fig. 2) (total number of individuals scanned held constant). Estimates from both top models indicated that our variable for reactionary responses to risky events was mainly informative due to the inclusion of intergroup encounters and the immediate aftermath (20 min) of those events. Coefficients in these two models were the same ($\beta \pm SE = 0.364 \pm 0.076$) and their 95% confidence intervals differed only slightly (model 1: 0.215, 0.514; model 3: 0.211, 0.509).

We used model 3 to estimate the predicted change in the number of neighbours per scan sample during encounters to account for location-specific risk. During intergroup encounters, the Barn group gained about four to five individuals per sample ($\widehat{y} = 4.865$, 95% PI: 3.852, 6.077) while the House group gained about three individuals ($\widehat{y} = 3.249$, 95% PI: 2.543, 4.107). Counts of neighbours were somewhat elevated 20 min following these events (Barn: $\widehat{y} = 1.328$, 95% PI: 0.632, 2.206; House: $\widehat{y} = 0.887$, 95% PI: 0.427, 1.479), but samples at 40 and 60 min overlapped baseline values.

Eagle encounters did not apparently elicit any change in cohesion over baseline values (model 1: $\beta \pm SE = 0.02426 \pm 0.099$; model 3: $\beta \pm SE = 0.020 \pm 0.098$), and there was no apparent change in cohesion in the 20, 40 or 60 min after these events (Fig. 2).

Hypothesis 2: Samangos Pre-emptively Alter Spatial Cohesion in Response to Location-specific Risk in the Absence of Any Direct Threat

In the absence of any direct threat (holding the 'event' variable at baseline/reference values), relative intergroup encounter risk was not strongly associated with the number of neighbours/spatial cohesion, and values in high-risk locations overlapped with low risk ($\beta \pm SE = 0.209 \pm 0.287$, 95% CI: -0.354, 0.763) (Fig. 3).

In contrast, we found an apparently positive association with increasing eagle risk. The coefficient for this term in model 3 overlapped zero ($\beta \pm SE = 0.89 \pm 0.51$, 95% PI: -0.11, 1.89), which may reflect differences between the two samango groups in their response. In areas of the highest risk (upper quartile), the Barn group tended to have about five to six more nearest neighbours within a scan sample than when in areas with the lowest risk ($\widehat{y} = 5.788$, 95% PI: 2.946, 9.678). The House group tended to have about four more individuals ($\widehat{y} = 4.105$, 95% PI: 0.760, 6.848)

Table 2
Model selection criteria and models ranked by weight and evidence ratios

Model	K	loglik	AICc	Δ_i	ω_i	Ev. Rat	Marginal - pseudo R^2 %	Conditional - pseudo R^2 %
1	**19**	**-3794.62**	**7627.91**	**0.00**	**0.57**	**1.00**	**13.59%**	**53.01%**
3	**21**	**-3792.88**	**7628.602**	**0.69**	**0.41**	**2.25**	**14.44%**	**54.06%**
0	11	-3806.63	7637.57	9.64	0.0046	124.41	11.62%	53.03%
5	12	-3806.08	7638.38	10.47	0.0031	188.45	12.63%	54.18%
6	12	-3808.36	7639.05	11.14	0.0022	262.78	11.72%	54.82%
4	13	-3805.77	7639.92	12.01	0.0014	406.34	12.37%	54.03%
7	14	-3807.89	7640.06	12.15	0.0013	436.07	12.73%	53.76%
8	14	-3806.65	7641.68	13.77	0.0006	977.68	11.92%	53.17%
2	35	-3788.08	7648.46	20.55	0.0000	29020	14.61%	53.48%

Potential top models (1, 3), shown in bold, had a Δ_i of less than 6 and the null. All models contained the random effects and the fixed effects of group, proportion of sampled individuals engaged in social behaviour and the number of within-group aggressions that had occurred up to that time point. K represents the number of parameters; loglik is the log likelihood; AICc is the small-sample corrected Akaike information criterion; Δ_i is the change in AICc; ω_i is the model weight; Ev. Rat. is the evidence ratio calculated by dividing the model with the highest weight by the weight of the candidate model.

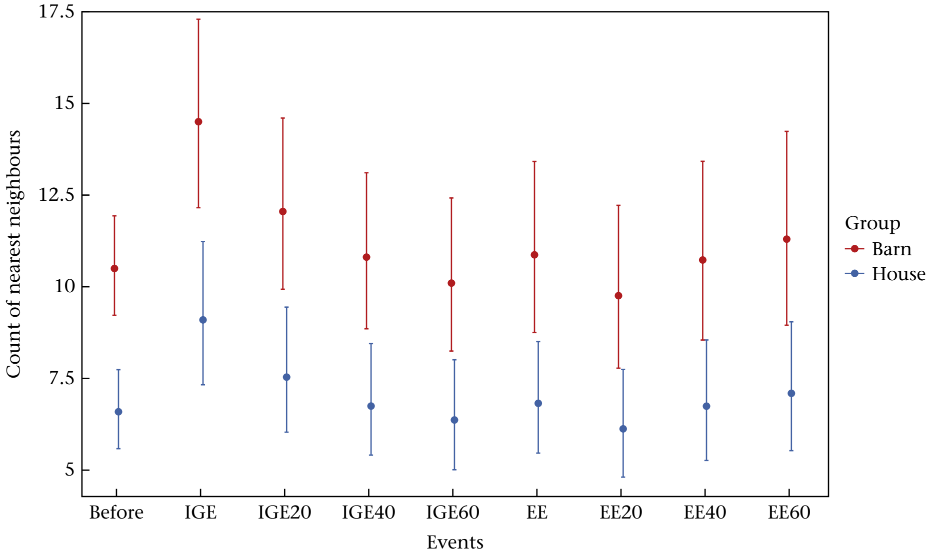

Figure 2. Counts of nearest neighbours per scan sample for both groups for baseline observations, intergroup encounters (IGE) and eagle encounters (EE) and for behavioural samples collected 20, 40 and 60 min following each type of event. This calculation holds the total number of individuals sampled constant at its mean. Both groups tended to be more cohesive during intergroup encounters (*N* = 45 for House and *N* = 99 for Barn). We sampled individuals within the House group as having fewer neighbours than the Barn group. Eagle encounters (*N* = 40 for House and *N* = 34 for Barn) did not apparently elicit a change in neighbours compared to baseline levels. Fitted counts are based on marginal averages from model 3. Bars represent 95% prediction intervals.

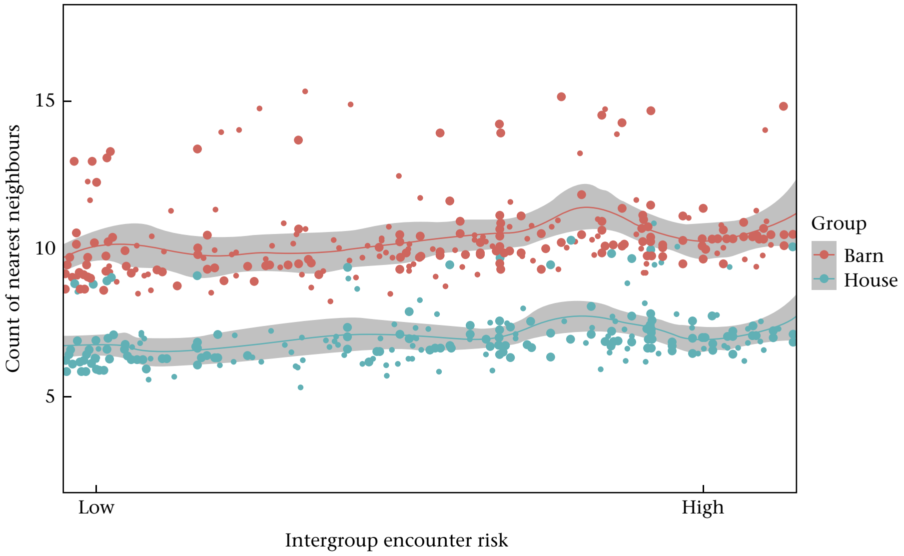

Figure 3. Predicted counts of neighbours under varying intergroup encounter risk based on model 3. Both groups showed little increase in cohesion over baseline values, even in areas of highest risk. The line represents the mean and the surrounding shaded areas represent 95% prediction intervals of the mean.

(Fig. 4), but its lower prediction interval was close to zero (as compared to baseline).

We originally predicted that if an encounter event occurred in a high-risk location, pre-emptive responses could remove the need for reactionary ones. To investigate this, we calculated predicted values for encounters only in areas of lowest risk. Reactions by the Barn group to intergroup encounters in low-risk areas resulted in an increase by about four neighbours per sample ($\hat{y} = 4.734$, 95% PI: 3.554, 6.349) and this was roughly the same as in high-risk locations ($\hat{y} = 4.852$, 95% PI: 3.662, 6.321). Reactions by the House group resulted in an increase of about three individuals in both low-risk ($\hat{y} = 3.162$, 95% PI: 2.081, 4.223) and high-risk locations ($\hat{y} = 3.241$, 95% PI: 2.416, 4.273). Similarly, we found no change to samango responses to eagle encounters while in low-risk locations (first quartile) (Barn group: $\hat{y} = 0.017$, 95% PI: -0.71, 1.053; House group: $\hat{y} = 0.012$, 95% PI: -0.426, 0.629). As only a few points existed with relative risk of zero, we could not examine changes at the minimum value.

DISCUSSION

We investigated whether samango monkeys would flexibly adjust their group spatial cohesion in response to immediate changes in ecology and whether groups would respond pre-emptively based on previous experience at a particular location. In the absence of any immediate events (intergroup or predator encounters), and when both location-specific risk and the proportion feeding were held constant at their means, our two groups

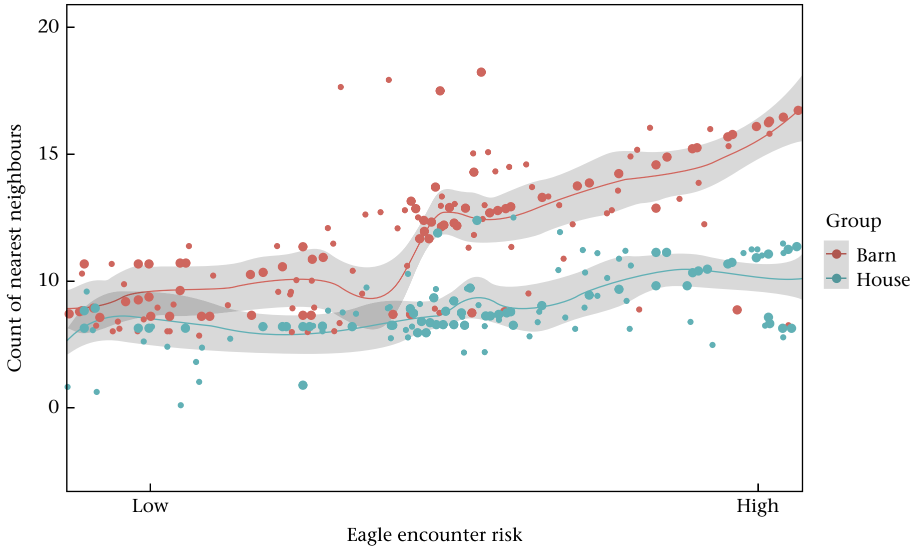

Figure 4. Predicted counts of neighbours under varying eagle encounter risk based on model 3. Both groups tended to be more cohesive under heightened eagle risk, but this effect was stronger for the Barn group versus the House group. The line represents the mean value and the surrounding area is its 95% prediction interval.

tended towards different levels of cohesion. Specifically, individuals within our House group tended to have fewer neighbours than individuals within our Barn group. Yet, both similarly displayed reactive responses to intergroup conflict and no apparent response to eagle encounters. Neither group strongly increased cohesion in areas of high intergroup encounter risk, but we found a slight positive trend, potentially indicating why this variable appeared in our top model set. In contrast, the Barn group may have pre-emptively increased cohesion in areas of high eagle risk, but we found less evidence that the House group responded similarly. Finally, reactionary responses to both intergroup encounters and eagle encounters were similar regardless of the level of location-specific risk.

Hypothesis 1

Intergroup encounters often resulted in individuals collectively making threats and chasing members of the competing group. For an individual, attacking a competing group may be less risky while in greater proximity to other groupmates (Eckhardt et al., 2015). Additionally, because many individuals target competitors simultaneously, spatial cohesion is likely to be high during these events. This result contrasts with our findings for immediate risk for eagle encounters where we did not detect substantial changes in cohesion for either group. This was unexpected given that previous studies have found that risk from aerial predators may be a stronger predictor than intergroup conflict or resource availability for space use in samangos at this site (Coleman & Hill, 2014a). Under immediate predation risk, we expected that subjects would seek proximity to conspecifics or that many individuals would seek cover in similar locations, resulting in increased cohesion. This finding that cohesion did not immediately increase is also in line with previous findings for blue monkeys; Treves (1998) found that elevated risk perception was associated with greater numbers of nearest neighbours, but also that individuals did not increase their spatial cohesion following playbacks of predator sounds (Treves, 1999). Similarly, in a study of grey-cheeked mangabey, *Lophocebus albigena*, reactions to crowned eagles, Arlet and Isbell (2009) found that the most commonly observed reaction to eagle predation attempts was sitting still. While Schreier and Swedell (2012) found that hamandryas baboons were more cohesive in the mornings following predator encounters, their observations were recorded in the hours following a threat, suggesting that longer-term perceptions of risk, rather than the immediate reaction to a predator encounter, resulted in increased cohesion. Thus, while increased numbers of nearest neighbours may provide enhanced access to social information that could mitigate risk (Fernández-Juricic & Kacelnik, 2004), reactively increasing cohesion may not be an effective strategy for this primate species to avoid mortality from aerial predators.

Hypothesis 2

Variables for both forms of location-specific relative risk measured here were included in the top model set. Increasing eagle risk was associated with an increase in cohesion for the Barn group but this was only weakly true for the House group. In comparison, we did not find strong support for an association between intergroup encounter risk and cohesion. However, we cannot rule out that a weak effect may be more pronounced in a study including more than two interacting habituated groups or a greater sample size. Thus, we found some mixed evidence for cohesion being sensitive to long-term variation in risk. This difference between risk from predation versus competitors may reflect the fact that conflict between groups does not always result in direct physical aggression. Additionally, if groups are able to hear an oncoming group from a distance and their reactions lead to greater cohesion, then pre-emptive responses may not always be necessary. In contrast, if reactive changes in cohesion do not help individuals evade aerial predators, pre-emptive responses may still reflect landscape-level variation in risk perception and could help individuals learn about the presence of predators more quickly. Once an aerial predator or alarm is detected, individuals might choose to remain still if moving makes them more conspicuous.

We used our model including both relative risk and event variables to assess whether pre-emptive increases in cohesion in high-risk locations would render reactionary responses unnecessary but found no evidence to support this prediction. Future studies using methods other than direct observation might investigate this with risk from terrestrial carnivores as our sample size allowed us to focus on risk only from eagles (LaBarge, Hill, Berman, Margulis, & Allan, 2020). Strategies for evading other predators could also include a greater reactionary change in cohesion.

These results, combined with previous studies on samangos avoiding areas of high perceived predation risk (Coleman & Hill, 2014a), may indicate that this species can remember where they have previously encountered danger. Evidence from other species, including other primates, suggests that this is plausible (Cunningham & Janson, 2007; Fagan et al., 2013; Garber, 1989). Thus, further investigation into the role of spatial memory in predation or conflict avoidance may be a promising area of future research.

Additional Ecological Variables

Habitat attributes, including horizontal visibility and canopy cover, are often associated with predation risk (Fortin et al., 2009) and the ability of individual animals to monitor one another (Fernández-Juricic & Kacelnik, 2004; Frechette, Sieving, & Boinski, 2014), but our models that included interactions between location-specific risk or risky events and habitat attributes (models 2, 7–8) had relatively low weights. This was unexpected because previous studies of predation on forest primates indicated that crowned eagles often attack where canopy cover is relatively low (Shultz, 2001) and previous studies on this population indicated that understory visibility is a significant predictor of perceived risk (Coleman & Hill, 2014a; Emerson, Brown, & Linden, 2011). A possible explanation for this is that subcanopy structure and the presence of sturdy branches to perch and ambush monkeys are also important for how successful an eagle might be in an attack. Additionally, while we used similar visibility sampling methods as Coleman and Hill (2014a), understory visibility may be more important for risk from terrestrial predators. We did not attempt to sample risk from these predators because encounters were too infrequent and our presence during observations may have modulated risk from these species because many terrestrial carnivores are intolerant of proximity to people (Ngoprasert, Lynam, & Gale, 2007; Smith et al., 2017). Furthermore, previous studies on this population indicate that humans might reduce samango risk perception of these terrestrial carnivores while observed (Nowak et al., 2014). This could mean that risk landscapes or within-group spatial patterns are significantly different for these groups when they are not in proximity to humans. Risk landscapes for intergroup encounters may also differ because unhabituated primates often avoid contact with humans (Williamson & Feistner, 2003). Thus, future research should attempt to measure cohesion through means other than direct observation such as using high fix-rate GPS collar data or coupling GPS collar locations with data from proximity sensors (Handcock et al., 2009).

We included the proportion of the group feeding on important fruiting trees as a control variable in all our models. While this variable was not significant, we did find a small positive trend in our marginal effects where cohesion increased along with this variable. While beyond the scope of this study, it is possible that a finer-scale examination of individual feeding trees might reveal greater differences if we did not group several different large and productive food trees for this variable. Additionally, examination of the control variables for within-group behaviour (affiliative social and aggression) revealed that both are likely important for overall cohesion. Here we aimed to control for these effects because our focus was on a proxy for overall group spatial cohesion and because each unit of our response variable comprised many different individuals from different positions within a group. Yet, it is likely that more individual-based analyses in many primates would find additional characteristics such as age, rank or personality characteristics important for cohesion. Interestingly, we found that cohesion seemed to increase when more within-group aggression was recorded. Future studies might attempt to examine how risk from within a social group could affect an individual's decision to remain close to conspecific neighbours. However, as previously noted, if a study species is predated on by human-intolerant carnivores but experiences a ‘human-shield’ while observed, subjects may perceive this change (Nowak et al., 2014). This may mean results could inflate the way in which animals respond to within-group risk because they may face less risk from outside the group. This could also apply to risk from unhabituated groups of the same species. One workaround to this problem could be the use of camera traps for measuring number of neighbours or another proxy for spatial cohesion. For example, McCarthy et al. (2019) were able to use images for creating social networks of party association in wild chimpanzees, which has been typically measured through direct observation. While camera trapping for studying primate social behaviour is relatively new, these methods could offer a solution when direct observation could alter risk (LaBarge et al., 2020).

Behavioural differences between groups are often attributed to group size without accounting for predominant ‘personality’ types of individuals (individual-level behavioural traits that are repeatable across time) across the group (Keiser & Pruitt, 2014). Thus, these observed differences in absolute number of neighbours might be due to differences in individuals' perception of risk, group composition, or a combination of factors. It should also be noted that while our larger group was approximately double the size of our smaller study group, both were large compared with other studied populations of Sykes' monkey, *C. albogularis* (Cowlishaw et al., 2004) or blue monkey (*C. mitis*; previously considered conspecific with samangos) (Cords, 2012). One difference between our two groups was that the Barn group used a smaller total ranging area during the study period (147.15 ha versus 237.66 ha for the House group, September 2015 – December 2017) while encountering a similar number of eagles over the period used to construct the risk landscapes. This could mean that the Barn group was more cohesive during most baseline observations because avoidance of risky locations was more difficult.

Conclusions

Spatial cohesion is important for the stability of animal groups and for effective social information transfer about risks or resources (Evans et al., 2016; Frechette et al., 2014), but local environmental conditions may affect the costs and benefits of remaining near groupmates. Cohesion in samangos is an apparently flexible characteristic that changes reactively to encounters with competing groups but not to immediate predation risk from eagles. Whether this is also true with terrestrial predators is uncertain, but future studies using methods other than direct observation of habituated subjects might be better suited to answer that question.

Our results indicating pre-emptive changes associated with eagle risk suggest that this species might recall attributes of risky locations. This is unsurprising given previous evidence that samangos avoid areas on the landscape where they face greater risk from eagles (Coleman & Hill, 2014a). Yet, few studies focused on animal ‘landscapes of fear’ have attempted to infer mechanisms underlying spatial variation in predation avoidance or antipredator behaviours. Future studies might explicitly consider the relative contributions of habitat attributes and the memory of previous encounters using field experiments with cues from predators or competitors.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2020.03.005.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*, 227–267.

Anderson, D., & Burnham, K. (2004). *Model selection and multi-model inference* (2nd ed.). New York, NY: Springer-Verlag.

Arias-Del Razo, I., Hernández, L., Laundré, J. W., & Velasco-Vázquez, L. (2012). The landscape of fear: Habitat use by a predator (*Canis latrans*) and its main prey (*Lepus californicus* and *Sylvilagus audubonii*). *Canadian Journal of Zoology, 90*(6), 683–693.

Arlet, M. E., & Isbell, L. A. (2009). Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology, 63*(4), 491.

Benadi, G., Fichtel, C., & Kappeler, P. (2008). Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology, 70*(10), 956–965.

Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology, 76*(6), 1075–1085.

Bertram, B. C. (1978). Living in groups: Predators and prey. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (1st ed., pp. 64–96). Oxford, U.K: Blackwell Scientific.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution, 24*(3), 127–135.

Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences, 284*(1855), 20170449.

Brewer, M. J., Butler, A., & Cooksley, S. L. (2016). The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. *Methods in Ecology and Evolution, 7*(6), 679–692.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology, 82*(5), 1098–1105.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal, 9*(2), 378–400.

Brower, J. E., Zar, J. H., & von Ende, C. N. (1998). *Field and laboratory methods for general ecology*. Boston, MA: McGraw-Hill.

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour, 85*(4), 807–816.

Bryer, M. A., Chapman, C. A., & Rothman, J. M. (2013). Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour, 150*(3–4), 277–293.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23–35.

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology, 96*(9), 2370–2382.

Calenge, C. (2006). The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling, 197*(3–4), 516–519.

Chivers, D. P., Brown, G. E., & Smith, R. J. F. (1995). Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): Implications for antipredator behaviour. *Canadian Journal of Zoology, 73*(5), 955–960.

Coleman, B. T., & Hill, R. A. (2014a). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour, 88*, 165–173.

Coleman, B. T., & Hill, R. A. (2014b). Biogeographic variation in the diet and behaviour of *Cercopithecus mitis*. *Folia Primatologica, 85*(5), 319–334.

Cords, M. (2012). The 30-year blues: What we know and don't know about life history, group size, and group fission of blue monkeys in the Kakamega Forest, Kenya. In P. M. Kappeler, & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 289–311). Berlin, Germany: Springer.

Cowlishaw, G., Lawes, M. J., Lightbody, M., Martin, A., Pettifor, R., & Rowcliffe, J. M. (2004). A simple rule for the costs of vigilance: Empirical evidence from a social forager. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 271*(1534), 27–33.

Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences of the United States of America, 105*(2), 577–581.

Cunningham, E., & Janson, C. (2007). Integrating information about location and value of resources by white-faced saki monkeys (*Pithecia pithecia*). *Animal Cognition, 10*(3), 293–304.

Dall, S. R., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution, 20*(4), 187–193.

Dröge, E., Creel, S., Becker, M., Christianson, D., M'Soka, J., & Watson, F. (2019). Response of wildebeest (*Connochaetes taurinus*) movements to spatial variation in long term risks from a complete predator guild. *Biological Conservation, 233*, 139–151.

Eckhardt, N., Polansky, L., & Boesch, C. (2015). Spatial cohesion of adult male chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology, 77*(2), 125–134.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews, 64*(1), 13–33.

Emerson, S. E., Brown, J. S., & Linden, J. D. (2011). Identifying Sykes' monkeys', *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Animal Behaviour, 81*(2), 455–462.

Evans, J. C., Votier, S. C., & Dall, S. R. (2016). Information use in colonial living. *Biological Reviews, 91*(3), 658–672.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., et al. (2013). Spatial memory and animal movement. *Ecology Letters, 16*(10), 1316–1329.

Fernández-Juricic, E., Beauchamp, G., & Bastain, B. (2007). Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Animal Behaviour, 73*(5), 771–778.

Fernández-Juricic, E., & Kacelnik, A. (2004). Information transfer and gain in flocks: The effects of quality and quantity of social information at different neighbour distances. *Behavioral Ecology and Sociobiology, 55*(5), 502–511.

Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology, 90*(9), 2480–2490.

Frechette, J. L., Sieving, K. E., & Boinski, S. (2014). Social and personal information use by squirrel monkeys in assessing predation risk. *American Journal of Primatology, 76*(10), 956–966.

Freedman, D. A., & Freedman, D. A. (1983). A note on screening regression equations. *American Statistician, 37*(2), 152–155.

Furrer, R. D., Kyabulima, S., Willems, E. P., Cant, M. A., & Manser, M. B. (2011). Location and group size influence decisions in simulated intergroup encounters in banded mongooses. *Behavioral Ecology, 22*(3), 493–500.

Garber, P. A. (1989). Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Primatology, 19*(4), 203–216.

Grey, J. N. C., Bell, S., & Hill, R. A. (2017). Leopard diets and landowner perceptions of human wildlife conflict in the Soutpansberg Mountains, South Africa. *Journal for Nature Conservation, 37*, 56–65.

Handcock, R., Swain, D., Bishop-Hurley, G., Patison, K., Wark, T., Valencia, P., et al. (2009). Monitoring animal behaviour and environmental interactions using wireless sensor networks, GPS collars and satellite remote sensing. *Sensors, 9*(5), 3586–3603.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ, 2*, e616.

Hartig, F. (2017). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (R package version 0.1, 5) https://CRAN.R-project.org/package=DHARMa.

Heesen, M., Macdonald, S., Ostner, J., & Schülke, O. (2015). Ecological and social determinants of group cohesiveness and within-group spatial position in wild assamese macaques. *Ethology, 121*(3), 270–283.

Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science, 269*(5228), 1260–1262.

Henzi, S. P., Payne, H., & Lawes, M. (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour, 140*(4), 453–471.

Hijmans, R. J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., et al. (2017). *Raster: Geographic data analysis and modeling (*R Package Version 2.9.5*)*. https://CRAN.R-project.org/package=raster.

Isbell, L. A., & Enstam, K. L. (2002). Predator (in)sensitive foraging in sympatric female vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*): A test of ecological models of group dispersion. In L. E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 154–168). New York, NY: Cambridge University Press.

Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. *Behaviour, 105*(1–2), 53–76.

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: Foraging costs and predation risks. *Behavioral Ecology, 6*(3), 326–336.

Keiser, C. N., & Pruitt, J. N. (2014). Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proceedings of the Royal Society B: Biological Sciences, 281*(1796), 20141424.

King, A. J., Wilson, A. M., Wilshin, S. D., Lowe, J., Haddadi, H., Hailes, S., et al. (2012). Selfish-herd behaviour of sheep under threat. *Current Biology, 22*(14), R561–R562.

LaBarge, L. R., Hill, R. A., Berman, C. M., Margulis, S. W., & Allan, A. T. (2020). Anthropogenic influences on primate antipredator behavior and implications for research and conservation. *American Journal of Primatology, 82*(2). e23087.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology, 79*(8), 1401–1409.

Lawes, M. J., & Henzi, S. P. (1995). Inter-group encounters in blue monkeys: How territorial must a territorial species be? *Animal Behaviour, 49*(1), 240–243.

Lüdecke, D. (2018). *sjstats: Statistical functions for regression models* (R package version 0.14.0) https://CRAN.R-project.org/package=sjstats.

McCarthy, M. S., Després-Einspenner, M. L., Farine, D. R., Samuni, L., Angedakin, S., Arandjelovic, M., et al. (2019). Camera traps provide a robust alternative to direct observations for constructing social networks of wild chimpanzees. *Animal Behaviour, 157*, 227–238.

Müller, C. A., & Manser, M. B. (2007). 'Nasty neighbours' rather than 'dear enemies' in a social carnivore. *Proceedings of the Royal Society B: Biological Sciences, 274*(1612), 959–965.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133–142.

Ngoprasert, D., Lynam, A. J., & Gale, G. A. (2007). Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx, 41*(3), 343–351.

Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P., & Hill, R. A. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology, 25*(5), 1199–1204.

Payne, H. F., Lawes, M. J., & Henzi, S. P. (2003). Fatal attack on an adult female *Cercopithecus mitis erythrarchus*: Implications for female dispersal in female-bonded societies. *International Journal of Primatology, 24*(6), 1245–1250.

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *R Journal, 10*(1), 439–446.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Radford, A. N., Majolo, B., & Aureli, F. (2016). Within-group behavioural consequences of between-group conflict: A prospective review. *Proceedings of the Royal Society B: Biological Sciences, 283*(1843), 20161567.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology, 86*(10), 2805–2814.

Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology, 65*(1), 77–89.

Rueden, C. T., Schindelin, J., Hiner, M. C., DeZonia, B. E., Walter, A. E., Arena, E. T., et al. (2017). ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics, 18*(1), 529.

Schreier, A. L., & Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *American Journal of Physical Anthropology, 148*(4), 580–588.

Shopland, J. M. (1982). An intergroup encounter with fatal consequences in yellow baboons (*Papio cynocephalus*). *American Journal of Primatology, 3*(1-4), 263–266.

Shultz, S. (2001). Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia Primatologica, 72*(4), 248–250.

Shultz, S., Noë, R., McGraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 271*(1540), 725–732.

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., et al. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences, 284*(1857), 20170433.

Sugiura, H., Shimooka, Y., & Tsuji, Y. (2011). Variation in spatial cohesiveness in a group of Japanese macaques (*Macaca fuscata*). *International Journal of Primatology, 32*(6), 1348–1366.

Treves, A. (1998). The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour, 135*(4), 453–481.

Treves, A. (1999). Vigilance and spatial cohesion among blue monkeys. *Folia Primatologica, 70*(5), 291–294.

Trillmich, J., Fichtel, C., & Kappeler, P. M. (2004). Coordination of group movements in wild Verreaux's Sifakas (*Propithecus verreauxi*). *Behaviour, 141*(9), 1103–1120.

Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology, 90*(2), 546–555.

Williamson, E. A., & Feistner, A. T. (2003). Habituating primates: Processes, techniques, variables and ethics. In J. M. Setchell, & D. J. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide* (pp. 25–39). Cambridge, U.K.: Cambridge University Press.

Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour, 83*(1), 277–291.

Zhao, J. M., Lyu, N., Sun, Y. H., & Zhou, L. Z. (2019). Number of neighbors instead of group size significantly affects individual vigilance levels in large animal aggregations. *Journal of Avian Biology, 50*(4). https://doi.org/10.1111/jav.02065.

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ORIGINAL ARTICLE

Extent of threat detection depends on predator type and behavioral context in wild samango monkeys groups

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Abstract

Detecting predators requires information, and many behavioral and environmental features are predicted to enhance or limit an animal's ability to learn about potential danger. Animals living in groups are thought to be at an advantage for learning about predator presence, but individual safety also depends on cues spreading from detectors to nondetectors as unsuspecting individuals may still be vulnerable. In this study, we simulated predator presence among two groups of wild samango monkeys (*Cercopithecus albogularis schwarzi*) to mimic natural encounters where only some individuals within a primate social group have access to personal information about potential threats. We did this using visual models of natural predators placed in positions for the monkeys to encounter within the landscape for a limited amount of time. We measured the number of individuals that were observed to detect and respond to these models with antipredator reactions, relative to subgroup size. While initial detectors that were able to spot the model themselves always reacted with overt behaviors such as alarm calling or staring at the model, responses did not typically spread to all group members. The number of initial detectors was also only weakly associated with the number of individuals that responded at the end of a trial. Initial responses to leopards were much stronger and more likely to spread than those given in response to pythons or eagles, and the importance of behaviors assumed to have an antipredator function depended on the type of predator the samangos encountered.

Significance statement

Early detection is critical for prey to survive an encounter with an ambush predator. Social prey have the advantage of being able to rely on cues from conspecifics, though individuals that do not detect a potential threat can still be susceptible to attack. Here, we exposed wild samango monkeys to predator models to simulate predator presence to only part of a social group. Habitat visibility was a key predictor affecting collective detection, but the importance of other hypothesized factors—scanning and group spatial cohesion—depended on the predator species. Overall, our results indicate that the social effectiveness of purported risk-sensitive strategies varies based on the type of threat encountered.

Keywords Predator detection · Antipredator behavior · *Cercopithecus albogularis* · Social information

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Introduction

In natural settings, the probability that most members of an animal group will respond to the presence of a predator prior to attack depends on multiple factors that can constrain or facilitate social information transfer. The outcome of information transfer from detectors to nondetectors is referred to as collective detection and is an important hypothesized benefit of group living for social vertebrates (Lima 1996; Bednekoff and Lima 1998). Early collective detection is especially important for avoiding mortality by ambush hunters that rely on remaining hidden until prey animals are within a certain distance (Caro 1995; Cresswell and Quinn 2010). When an ambush predator learns that prey animals are aware of its presence, it may give up on an attack that is likely to be unsuccessful (Woodland et al. 1980; Zuberbühler et al. 1999).

Learning about predator presence is constrained by individuals' abilities to monitor one another and the type of signal or cue given by an initial detector (Hochman and Kotler 2007; Pays et al. 2013). Local habitat characteristics, like visibility, should limit how quickly an initial detector can sense and respond to a threatening cue (Whittingham et al. 2004), but whether this information spreads throughout the rest of a group should also depend on the mechanism by which a species communicates alarm (e.g., visual cues or alarm calls) (Pays et al. 2013). General wariness or risk perceptions of group members might influence how much of a group is monitoring the environment versus engaged in other activities (Hochman and Kotler 2007) or how close individuals are to their conspecifics (Frechette et al. 2014; LaBarge et al. 2020a). Both factors are hypothesized to limit the ability of individuals to personally collect information about potential risks (Fernández-Juricic and Kacelnik 2004). However, several studies indicate that animals typically do not act on social sources of information as readily as they do on their own detection (Lima 1995; Kendal et al. 2004) and that more distant cues given by groupmates may be perceived as less reliable (King and Cowlishaw 2007). As such, the number of individuals who personally detect and conspicuously respond to a threat should subsequently determine whether nondetectors act on signals from conspecifics (King and Cowlishaw 2007; Ward et al. 2008).

In primates, information about predators is often conveyed through alarm calls that can reach a wide range of individuals (Caro 2005; Frechette et al. 2014). Emitting alarms can be risky if they attract the attention of an approaching predator but may also function to deter an attack if the signal informs a predator that it has been detected (Zuberbühler et al. 1999; Isbell and Bidner 2016; Adams and Kitchen 2018). These signals may also function to solicit collective action, such as mobbing, which may cause a predator to retreat (Isbell 1994; Arlet and Isbell 2009). Yet if an initial detection by one member goes unnoticed by the rest of the group, an ambush predator may be able to attack another unsuspecting individual (Lima 1995). In experiments in which individual birds foraging within flocks were exposed to visual cues indicating predator presence, collective responses were more likely when a greater number of individuals initially detected the stimulus and fled, whereas limited responses were common when only one individual was able to detect the cue (Lima 1995). Experiments with fish shoals have similarly revealed that group-wide antipredator reactions require that a threshold "quorum" number of individuals detect and respond to a cue before the rest of the group changes their behavior (Ward et al. 2008). In contrast, field experiments with primates have found evidence that alarms may function to alert nondetectors to a potential threat. Solitary male Thomas langurs (*Presbytis thomasi*) tend to alarm less to experimental tiger models than those within groups (Wich and Sterck 2003). Sooty mangabeys (*Cercocebus atys*) were more likely to emit an alarm to a model snake when fewer conspecifics were nearby at the encounter site and when others had not previously alarmed (Mielke et al. 2019). Similar experiments with chimpanzees (*Pan troglodytes*) and model snakes indicated that subjects were more likely to alarm when with another individual who had not previously encountered the potential threat (Crockford et al. 2012). While these studies focused on individual alarms rather than collective responses, they may indicate that primates are more likely to respond to distant signals if alarms function to inform nondetectors of a potential threat.

Naturally occurring encounters with ambush hunters tend to be brief, and this is especially true if conspicuous indications of detection lead to a predator giving up an attack (Caro 1995; Zuberbühler et al. 1999). In these scenarios, it is likely that the accessibility of cues about potential threats will be uneven within large social groups. Several studies have examined the time to predator detection in primates and other animals (e.g., Pays et al. 2013; Janson et al. 2014), but few to our knowledge have actually examined how much of a social group ends up detecting and responding to a predator during a brief encounter. In this study, we examined the contexts that lead to variation in detection of predators by wild samango monkey groups (*Cercopithecus albogularis schwarzi*). We did not aim to completely isolate personal or social information acquisition in our field study but aimed to mimic a natural scenario where several variables would lead to differences in the number of initial detectors (who could personally spot a predator) and subsequently enhance or limit responses spreading to other group members once a threat was no longer visible. Encounters with terrestrial predators were rare at our study site despite the resident leopard (*Panthera pardus*) population (Williams et al. 2017), probably due in part to the presence of humans (Isbell and Young 1993; Nowak et al. 2014). Therefore, we used experimental methods to overcome this issue following a long tradition of researchers using realistic looking visual models to simulate predator presence to wild primates (van Schaik and Mitrasetia 1990; Pereira and Macedonia 1991) and placed these in the landscape for an oncoming group to detect within a restricted time period. We chose visual models over auditory cues, because most group members would still be unaware of their presence even when one or more close individuals initially detected the potential threat (Arnold et al. 2008). Additionally, given that ambush predators often rely on surprise, the detection of cryptic or partially obscured visual cues would constitute a relatively natural situation.

Primate antipredator responses often vary with the predator's hunting mode and may also vary with the detectors' perception of danger (Seyfarth et al. 1980; Zuberbühler et al. 1999; Coss et al. 2007). Thus, responses that reach the greatest number of detectors may occur simply when appropriate predator-specific responses are especially conspicuous (e.g., loud alarm calling or mobbing) or may also occur in response to predators that are most feared. The three models we used were replicas of a crowned eagle (*Stephanoaetus coronatus*), leopard, and rock python (*Python sebae*). Among samango predators at our field site, eagles likely pose the greatest threat because previous studies on this population have determined that samangos' perception of eagle risk results in a "landscape of fear" in which individuals tend to avoid dangerous locations (Coleman and Hill 2014). Leopards also pose a risk, but it is likely that they only rarely hunt arboreal samangos (Williams et al. 2018). Finally, snakes pose a risk to many primates, and detection often results in antipredator reactions across a range of species (Shibasaki and Kawai 2009; Isbell and Etting 2017; Mielke et al. 2019), but it is uncertain what risk they pose to samangos relative to other predators. These three predators rely on concealment to attack unaware prey animals (Shultz 2001; Isbell and Bidner 2016), though eagles can either sit and wait in the forest canopy or attack on the wing (Shultz and Thomsett 2009).

Here, we test the hypothesis that characteristics of the social group, local environment, and perception of the predator encountered can constrain or facilitate information transfer within samango groups. Our response variable was the final number of individuals who reacted with risk-sensitive/antipredator behaviors at the end of a trial, relative to subgroup size. Critical to this study is that these experiments occurred on two large groups where most individuals could not personally detect our models within the time limit (see "Predator exposure"). Specifically, we predicted the number of detectors would increase during trials if (1) habitat visibility was high, (2) spatial cohesion, measured as the number of the nearest neighbors, was greater, (3) a greater proportion of the group was monitoring the environment prior to a trial, (4) more individuals could personally detect the threat themselves by being near the model before removal, and (5)predator-specific responses were especially conspicuous (alarm calling or other overt antipredator behaviors). Based on previous observational data, we predicted that the eagle would elicit the strongest reaction, followed by the leopard and then the python.

Methods

Study site and species

We conducted our study at the Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo Province, South Africa (23° 02′ S, 29° 26′ E). The study site encompasses an array of habitat types including tall moist Afromontane forest, deciduous woodland, acacia bush, and rocky grassland/cliffsides. We studied two samango groups, "Barn" group ($N \sim 45$) and "House" group ($N \sim 70$–80), that were well habituated to direct observation. Samango monkeys are medium-sized (adult females ~ 4.4 kg, adult males ~ 7.6 kg), arboreal guenons that live in single-adultmale–multifemale groups typically with 10 to 65 individuals (Coleman and Hill 2014). Groups were not always a single unit and would sometimes fission into one or more subgroups during the day. Mean (sub) group size at the beginning of trials was ~ 55 for the House group and ~ 40 for the Barn group. The House group contained 16 identifiable individuals, and the Barn group contained five. Observers could readily distinguish between age-sex classes. Natural predators of samangos at the site include crowned eagles (*S. coronatus)* and black eagles (*Aquila verreauxii*), African leopard (Williams et al. 2018), caracal (*Caracal caracal*) (Nowak et al. 2014), and rock pythons.

Predator models

Leopard and python models were realistic-looking plush toys, while the eagle model was created using a mesh wire, papier-mâché, and chicken feathers and painted to mimic the colors of a crowned eagle (Fig. S1). The leopard and eagle models were both larger than the python, reflecting their natural variation in size. Observers at this site have witnessed each of these predator types with one of these samango groups. To control for responses to novel but nonthreatening stimuli, we used a penguin model which does not resemble any bird native to the Soutpansberg.

Pilot trials

Between May and August 2017, we conducted pilot trials with our leopard model to assess whether samangos would respond to a visual model similarly to a live predator encounter. We used these preliminary trials to determine an adequate time between initial detection and covering the model that would minimize the possibility that the entire group could see it personally. This was necessary to avoid conflating social transmission of information with ongoing personal information acquisition. We placed the models approximately 100 m ahead of an oncoming group based on the direction individuals seemed to be moving, and finding it typically took 4–6 min following an initial detection for all of the remaining members of the (sub) group to respond. Detection was indicated by alarm calling, approaching, staring, and/or bobbing their heads at the model. Thus, we determined that an exposure of 90 s after the initial reaction would be enough time to ensure that much of the group could not see the model but that the response of the initial detector(s) would still be strong enough for others to respond.

Predator exposure

Following the pilot study, we conducted one or two predator model presentations per month on each group between June 2018 and June 2019. Experiments took place between 9:00 and 13:00. A research assistant followed the group from their sleeping site before dawn and collected behavioral data following the normal long-term research protocol (see “Behavioral data”). Communication between the assistant and experimental researchers via two-way radio allowed us to ensure that we did not place predator models during or following any natural predator encounters. Samango groups were generally cohesive (single group) but sometimes split into two or more subgroups. Our measure of “collective” detection (our dependent variable) was linked to the size of the observable (sub) group, rather than absolute group size. Therefore, prior to initiating the trials, observers recorded the number of visible individuals within the subgroup. This was completed by LRL and/or one or more field assistants.

We placed models beyond the visual range of the samango monkeys and approximately 75–150 m ahead of an oncoming group and according to the predator’s respective hunting styles. The eagle model was placed on a branch or large boulder > 2 m above the ground, the leopard was placed on the forest floor, and the python was placed either on the ground or on rocks/logs < 1 m from a ground level. Subsequently, observers that initiated the trial hid behind large rocks or trees to avoid subjects associating model predators with humans. Observers collecting general behavioral data made no attempt to conceal themselves. A video recording was made to confirm an identity and/orage-sex class for the initial detector (Sony Handycam). At the time of this initial detection, observers recorded the number of individuals within 25 m of the model (at the first detection and again at 90 s) and the ID and age-sex class of the detector(s). The mean distance of the initial detector from the predator model was 10.3 m (standard deviation (SD) 7.49 m) for the eagle, 19.3 m (SD 7.7 m) for the leopard, and 5.2 m (SD 4.6 m) for the python. All of these initial detectors were within the understory or subcanopy when we observed their response. Thus, it was unlikely that individuals beyond 25 m could typically personally detect a threat in this densely vegetated habitat. Immediately following the first detection of the model, the observers waited 90 s and then covered the model using a green canvas tarp. For leopard trials, the tarp was attached to ropes that allowed us to cover the model remotely. This was necessary because pilot trials indicated that detectors would approach this model, and we aimed to avoid being close to any of these individuals. For eagle and python trials, one of the observers would cover the model rapidly at 90 s. Once models were covered, observers continued to monitor groups for delayed responses and, when necessary, agreed on a final count of responders. Following trials, we used data from the nearest preceding group scan sample (collected between 5 and 15 min prior) to obtain information on relative levels of cohesion and scanning behavior (see “Behavioral data”).

In total, we completed 30 trials with 10 on each predator type (5 on each samango group). To control for potential reactions to novel stimuli, we also completed 10 trials with a nonthreatening bird model (penguin). We did not repeat trials on the same group in the same location (< 50 m) and recorded all the same behavioral and habitat data (see below) for both predator and control trials. Additionally, we left approximately two to three weeks, on average, between trials of the same predator type to minimize the potential for habituation. Our response measuring the variability in collective detection was the number of individuals within an immediate (sub) group reacting with obvious risk-sensitive behaviors before the end of a trial. We recorded the number of initial detectors and subsequently recorded the number of individuals who responded by the end of each trial. We note that these counts may slightly underestimate the true number as there may have been more responding individuals high in the trees or far out of sight.

Following each trial, we measured understory visibility by photographing a black and yellow 1 $m^2$225-square checkerboard 10 m from where the model was placed at 2 m high in each cardinal direction with the percentage of the squares visible recorded (each square = 6.6 cm^2) (LaBarge et al. 2020a). As groups tended to come down from the canopy during midmorning to lower forest strata, this was a good proxy for the degree of visibility most samangos would have in that habitat.

Every predator trial resulted in detection by at least one individual as indicated by alarm calling, visual inspection, head bobbing, and/or approaching the model. All but three of the initial detectors were unmarked individuals; however, in most of these unmarked individuals, observers could confirm that their age/sex class was different than previous detectors of the same predator type. The exceptions to this were two of the eagle trials which resulted in an initial detection by unidentified subadults from the “House” group and two of the leopard trials which resulted in detection by unidentified adult females in the "Barn" group. Because both groups were large and because we left three to four weeks between predator trials of the same type, it is likely that these were not the same individuals. One python trial in January 2019 was terminated early because the model fell out of a tree, resulting in immediate alarm calls from all visible "House" group members. We did not use data from this trial. The control model trials did not result in apparent behavior changes in adult or subadult individuals, but in three instances (two in the "House" group, one in the "Barn" group), juveniles approached the model on the ground and investigated it before moving on. Thus, we assumed that the novelty of predator models did not evoke antipredator reactions and that the responses recorded for other trials were appropriate for samangos encountering danger.

Behavioral data

Behavioral and location data were collected before, during, and following all predator trials via scan sampling (Altmann 1974) in a 5-min window every 20 min throughout the day. Day length ranged 10.5 h (06:40–17:20) to 14.5 h (04:40–19:00). Each sample location was recorded with a handheld GPS (Garmin GPSmap 60Cx or 62s, Garmin, Olathe, Kansas, US). Within a scan sample, we attempted to record the behavior of as many individuals as possible within the group and minimized repeating individuals by moving throughout the group and collecting data only when it is certain that an individual had not been previously observed (mean 10.8 individuals; range 6–14). Moving between spatial subsections and between the periphery and center of the group minimized oversampling intragroup cliques. Thus, these group scans were comprised of information on individuals found in various positions throughout the group. Within these samples, we recorded the date, time, group ID ("House" or "Barn"), individual age/sex class, and individual ID when known. For each subsampled individual, we recorded the number of noninfant neighbors each individual had within five meters (LaBarge et al. 2020a). Finally, we recorded whether an individual was scanning beyond an arm's reach (Treves 1998). Data from each of these individuals within a group scan was converted into a proportion (of 5sampled individuals) as a proxy for how much of the group was monitoring the environment or conspecifics prior to an initial detection. Blinded methods were not possible for this study as we collected data on wild, habituated animals in their native habitat.

Data availability

All data used in this manuscript and corresponding R code can be found within supplementary materials.

Analysis

To analyze these data, we used regression with a binomial distribution and logit link in the Stan computational environment accessed through the R package brms (Bürkner 2017). We considered the count of the number of individuals that responded as the number of k successes in a binomial trial (relative to n subgroup size). While frequentist methods might use an "exact" logit for small-sample data, Bayesian analysis can also improve accuracy and minimize the risk of type 1 and type M errors at small sample sizes by incorporating information about prior probabilities, along with the likelihood, to form a posterior probability distribution. For additional details on our model fitting methods, see supplementary materials (Detailed Analysis Methods).

We did not fit any random factors into our model because we did not knowingly repeat trials on the same initial detector. Additionally, our data were clustered into two groups which are too few levels to be included as a random factor. At best, random effects with too few levels produce similar estimates as models including the same term as a fixed effect (Moen et al. 2016). We assessed how much variation was due to "group" by calculating an intraclass correlation coefficient (ICC) with the package sjstats (0.24, Lüdecke 2018) and retained this in our model as a fixed effect as this would help account for this between-group variation in this repeated measures field experiment (Moen et al. 2016). Thus, we focus on population-level inferences and cannot make inferences about the differences between these two samango groups with this analysis.

Additional fixed effects were the categorical predator type (eagle, leopard, python, and control), percentage understory visibility, mean number of the nearest neighbors, the proportion of sampled individuals scanning/monitoring their surroundings, and the number of individuals within 25 m from the model at initial detection. The proportion scanning included individuals monitoring their surroundings or those that may have plausibly been looking in the direction of another monkey. We included "control" trials so that this categorical level could serve as a reference for the predator trials. The trial number was also included as a fixed effect to account for potential habituation to the same predator type. 80% of initial predator reactions came from adult female or subadult individuals; thus, we did not include age-sex class within our model. Results of previous studies led us to include interactions between the predator type and number of neighbors and the proportion of the group scanning (Whittingham et al. 2004; Frechette et al. 2014).

We used the Markov chain Monte Carlo (MCMC) sampling to obtain posterior estimates. We ran 450,000 iterations across five unthinned chains with a warmup of 425,000 for a total of 25,000 samples because larger effective MCMC sample sizes can produce more stable and reliable estimates for small-sample problems (Forster et al. 2003; Kruschke 2014)(Fig. S1). We checked model residuals using the package DHARMa (Hartig 2016) and applied posterior predictive checks with brms by visual inspection (Bürkner 2017). Variance inflation factor (VIF) was < 2.7 for all parameters, and Monte Carlo standard errors were all under 1%. Finally, we used 95% credible intervals (CIs) along with probability of direction (PD) values to evaluate the relative level of evidence for each parameter. PD values range from 50 to 100% and describe how much of a posterior distribution is entirely positive or negative. Here, we considered a parameter to have supporting evidence if a CI did not include zero and its PD was above 99.5%.

Results

The probability of an initial reaction spreading to more of the group depended on the predator type (Fig. 1, Table 1). In eagle trials, a mean of 25.9% (1.7–100%) of the "House" group and 39.7% (2.9–100%) of the "Barn" group responded during trials. In python trials, a mean of 14.7% (1.7–35%) of the "House" group and 32.6% (6.7–71.4%) of the "Barn" group responded and only one out of the total 10 trials resulted in more than 50% of the (sub) group clearly reacting. Responses to leopard models were more intense, and a mean of 80.80% (60–100%) of the "House" group responded and 63.56% (8.88–86.66%) of the "Barn" group responded to these trials. Only three out of the 30 predator trials resulted in 100% of visible subgroup members clearly responding—two of these responses were to eagle trials and one of these was to a leopard trial. Nevertheless, leopard responses were more consistently strong (resulting in more individuals responding overall) and contained an entirely positive CI and PD of 99.98% which was not the case for either the eagle or python.

Reactions to all three predator types resulted in alarm calls, but leopard trials resulted in individuals approaching the model from trees, potentially providing an additional auditory or visual cue to nondetectors that were able to view conspecifics, but not the predator model. Four of 10 leopard trials resulted in male "pyow" and "ant" alarm calls. We did not record any male alarms during eagle or python trials, but males are known to alarm at these predators during natural encounters. Males were typically found towards the center or rear of an oncoming group and, to our knowledge, were not the initial detectors in any of these trials (Table 1).

Greater visibility in understory habitat tended to positively predict wider responses overall (Fig. 2, Table 1); however, this trend was strong for just eagle and leopard trials. In contrast, the number of individuals within 25 m of the model during initial detection may have had a small positive effect on the percentage of the group engaged in antipredator responses at the end of the trial, although the CI for this value included zero and the PD for this parameter was lower than our threshold (Fig. S2, Table 1). We note that the mean number of individuals within 25 m at initial detection was 11.13% of the total subgroup and ranged from 2 to 28.8%. All of these individuals would have likely been able to personally detect the model before it was concealed after 90 s.

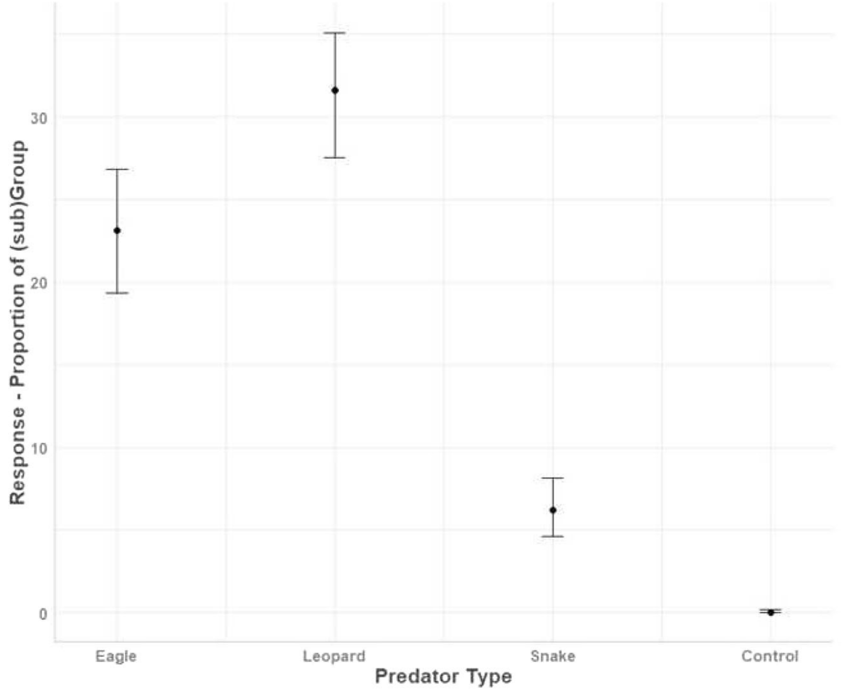


Fig. 1 Marginal effect plot of differences in response (proportion of (sub) group responding) between the predator types. All other predictors held at their mean or reference values. Bars represent 95% CI

Table 1 Coefficients from the joint posterior distribution, estimated errors, and 95% credible intervals. Num. w/in 25 m is the number of individuals near the predator model during the initial detection (max. end of apparent visual range). Scanning refers to the proportion of the sampled group scanning prior to the trial. Pred. type * neighbors refers to the interaction between the type of model predator and the number of nearest neighbors per individual. Pred. type * scanning refers to the interaction between the predator type and scanning. Rhat is the potential scale reduction factor on split chains which indicates convergence at 1.00 (Gelman-Rubin diagnostic). PD is the probability of direction where values above 99.5% are bolded

		Estimate	Est. error	L. 95%	U. 95%	Rhat	PD
Intercept		− 5.46	1.37	− 8.39	− 2.99	1	100.00%
Group		0.11	0.19	− 0.26	0.47	1	72.24%
Predator type	Eagle	1.93	1.38	− 0.57	4.88	1	93.02%
	Leopard	4.21	1.37	1.74	7.15	1	**99.98%**
	Snake	2.00	1.39	− 0.52	4.95	1	93.61%
Habitat visibility		2.73	0.8	1.18	4.30	1	**99.96%**
Num. of neighbors		− 1.28	0.98	− 3.42	0.46	1	91.92%
Num. w/in 25 m		0.05	0.02	− 0.00	0.10	1	97.06%
Scanning		− 0.69	1.22	− 3.19	1.63	1	71.17%
Trial number		− 0.11	0.06	− 0.22	− 0.00	1	97.61%
Pred. type * neighbors	Eagle	2.76	1.00	1.00	4.91	1	**99.91%**
	Leopard	1.51	0.98	− 0.22	3.66	1	95.39%
	Snake	1.99	0.99	0.25	4.14	1	98.86%
Pred. type * scanning	Eagle	1.28	1.28	− 1.14	3.90	1	84.55%
	Leopard	3.58	1.33	0.01	5.27	1	97.53%
	Snake	0.32	1.31	− 2.19	2.96	1	59.13%

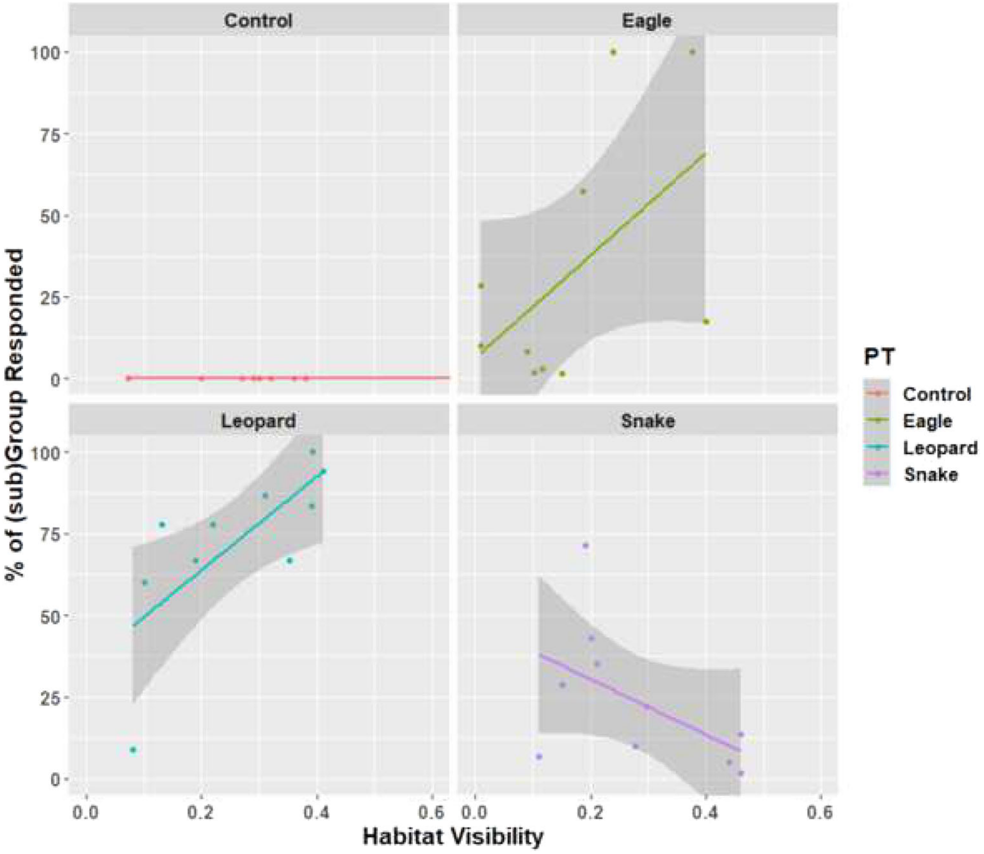


Fig. 2 Habitat visibility and the proportion of the group that responded at the end of a trial. PT is the predator type. The shaded area is 95% CI (credible interval)

Fig. 3 Proportion of sampled individuals scanning their environment/monitoring others prior to the trial and the percent of the group that responded. PT is the predator type. The shaded area is 95% CI

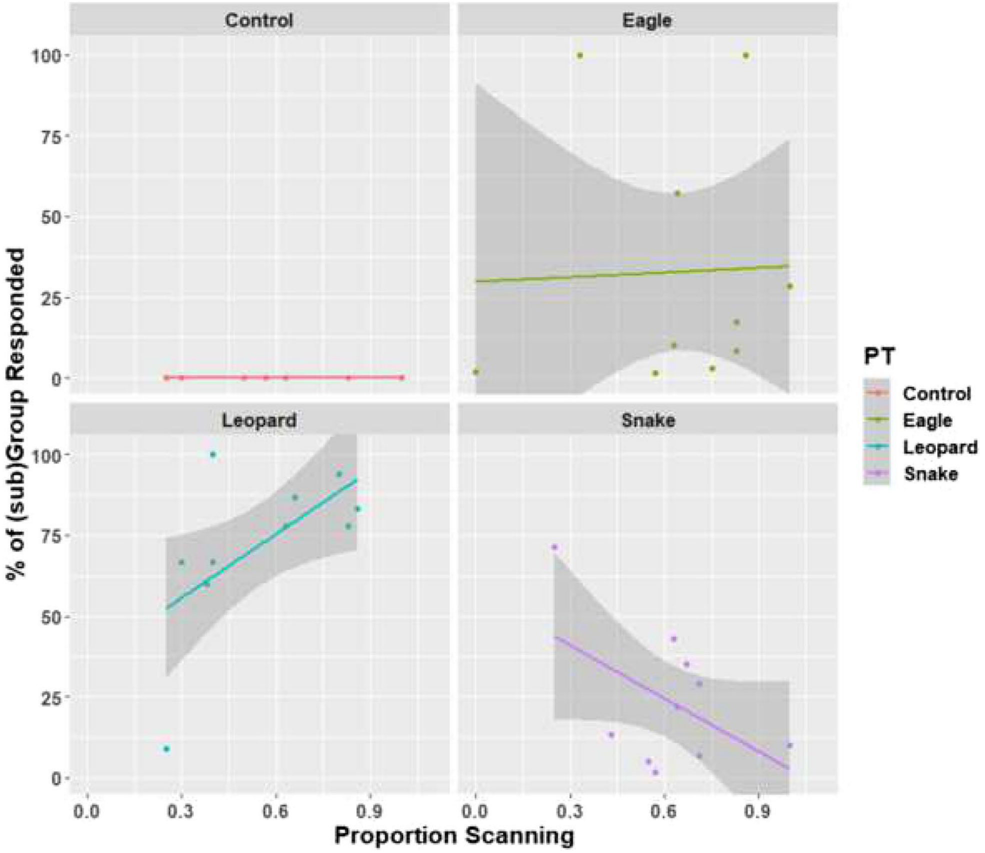
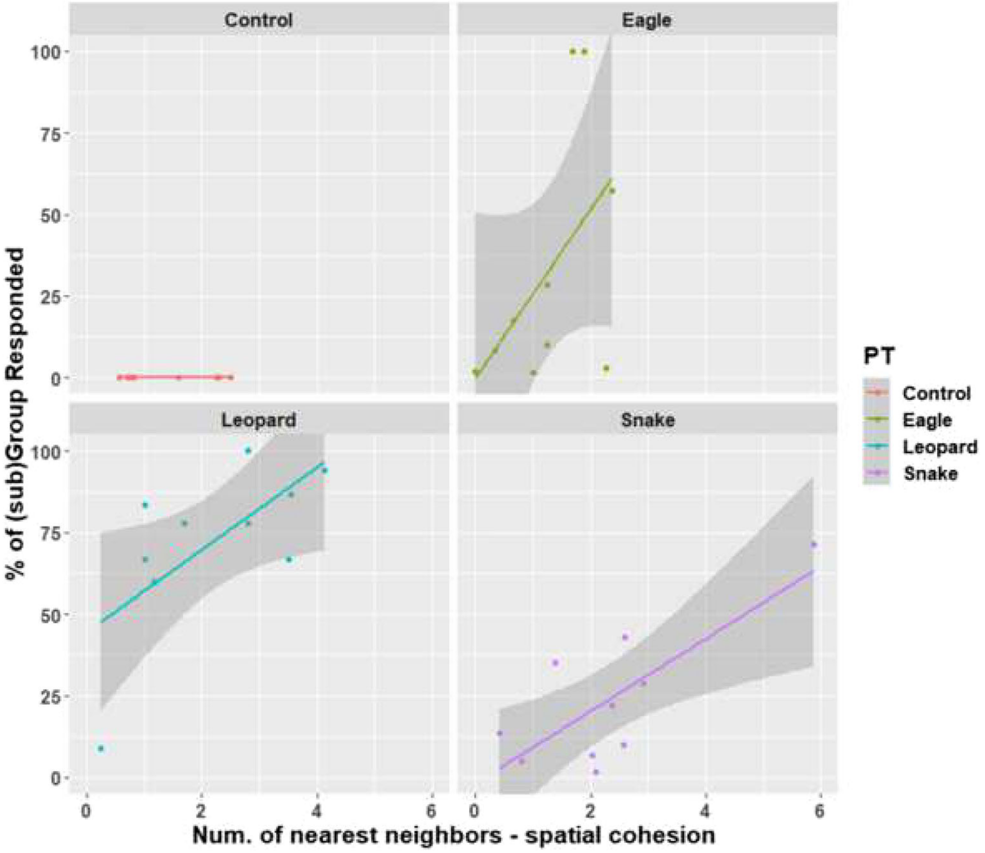


Fig. 4 Mean number of the nearest neighbors/individual prior to detection and percent of the group that eventually detected/responded. PT is the predator type. The shaded area is 95% CI



Interactions between scanning behavior or number of neighbors and models used revealed predator-specific differences. When a greater proportion of the group was engaged in scanning behavior prior to a leopard trial, more individuals tended to detect the model by the end, but this was not the case for the other predator types. Although this value had a PD below 99.5%, its CI did not cross zero (Fig. 3 and Table 1). Similarly, the number of neighbors (spatial cohesion) was apparently a positive predictor of widespread detection for eagle models and, potentially, python responses as well. However, while values tended to be positive for leopard trials (Fig. 4), there was less evidence overall (Table 1).

Although we could not test explicitly for differences between the two study groups, we had no evidence indicating substantial differences between them. The trial number was weakly negatively associated with the percentage of a group that would respond at the end of a trial but did not reach our importance threshold (Table 1, Fig. S3).

Discussion

While group living is hypothesized to be an effective strategy for mitigating predation risk, individuals within a group may still succumb to an attack if unaware of a predator. The goal of this study was to better understand whether factors hypothesized to facilitate or constrain information acquisition and transfer would predict the extent to which antipredator responses would spread in samango groups. Samango monkey groups that detected visual predator models reacted to all three with alarm calling, staring, and, in some cases, approaching the model, providing potential cues to nondetectors. Habitat visibility was a strong predictor of the outcome of our trials, potentially because more individuals were able to personally detect the model prior to the 90-s time limit. Yet the number of individuals that were likely able to detect the model personally—those within 25 m of it upon the first detection—was not a good predictor of the trial outcome. Given the size of our study groups, the density of these forest/acacia bush habitats, and time-limited predator exposures, most individuals would likely have had to rely on cues from conspecifics to learn about the potential threat. Thus, once initial detection had occurred, information about the threat would have to travel throughout the group. Additionally, we found that the effectiveness of purported risk-sensitive behavioral strategies which should enhance collective detection depended on the type of threat these samangos encountered. Specifically, scanning behavior prior to the trial was only a positive predictor for the extent of responses to leopard trials, but not the other predators. Spatial cohesion, as measured by the number of neighbors an individual had nearby (within 5 m), was also a potential predictor for group responses to the eagle or python models, but not the leopard. Finally, differences between the predator types (holding other variables constant) indicated that there were differences either in samango monkeys' ability to detect these predators or in the conspicuousness of predator-specific responses.

We assumed that high within-habitat visibility would lead to greater personal detection (prediction 1) but also that the number of individuals within close proximity to the model (< 25 m) at initial detection would positively predict the extent of responses due to the higher likelihood that these individuals could personally detect the model (prediction 4). Yet we found positive support only for the former. This result is consistent with experiments conducted with birds and fish that suggest the importance of personal information to group-wide predator detection (Lima 1995; Ward et al. 2008; Conradt 2011) but contrasts with experiments with other primate species in which individuals were more likely to alarm call when conspecifics were presumably unaware of a predator (Crockford et al. 2012; Mielke et al. 2019). Our result likely stemmed from visibility enhancing detection for a few initial detectors at the start of a trial but also allowed conspecifics to better monitor their neighbors. In this study, we were not able to repeatedly measure responses from the same known individuals over time due to habituation concerns and a relatively low number of consistently identified individuals within these study groups. Yet it is possible that potentially heritable interindividual differences in anxiousness or similar traits would result in certain individuals being particularly reactive (Brent et al. 2014; Watson et al. 2015). If this information was known to conspecifics, it could have influenced overall responses (Couchoux et al. 2018).

Many studies have suggested that social information is often perceived as less accurate than personal information (Kendal et al. 2004; King and Cowlishaw 2007). The exception to this may be that individual prey animals are more likely to act on social information when it comes from neighbors at close distance (Fernández-Juricic and Kacelnik 2004). Frechette et al. (2014) found that groups of squirrel monkeys (*Saimiri sciureus*) were more likely to react with escape responses to predator encounters when group spatial cohesion (measured as group spread) was high. Cohesion itself is likely also important for baseline levels of risk perception (Treves 1998; Fernández-Juricic et al. 2007), because individuals with more neighbors are hypothesized to be able to learn about potential threats earlier than individuals further from groupmates (prediction 2). We only found support for cohesion enhancing responses to eagle and snake models. Personal detection of these two predators may have been more challenging if they were better hidden within these densely vegetated habitats (Fig. S1) as detection distance and the extent of collective response tended to be greater for leopard trials. Thus, social information may have been more important to the outcome of eagle or snake trials compared with leopard trials. This may also explain why scanning behavior was a good predictor for the outcome of leopard trials, but not eagle or snake trials (prediction 3).

Trials with leopard models were the only ones that elicited consistently extensive responses and male alarm calls, although male responses were likely due to greater detection distances and the tendency for samango males to occupy positions near the center or rear of the group during the trials (LRL, personal obs.). This particular result does not fit with our initial prediction that perceived risk would be highest for eagles based on previous studies indicating their importance for samango landscape use (prediction 5; Coleman and Hill 2014). This is compared with responses of vervets (*Chlorocebus pygerythrus*) at this site who appear to preferentially avoid high leopard and baboon risk but do not respond similarly to eagle risk (Willems and Hill 2009). One potential explanation is that the postdetection strategies for avoiding these predators differ in their conspicuousness, because alarm calls and other overt antipredator reactions can serve as a particularly effective predator deterrent for leopards (Woodland et al. 1980; Isbell and Bidner 2016; Adams and Kitchen 2018). As such, widespread and repeated alarm calling may not deter eagles or snakes to the same extent. In each leopard trial, detecting individuals also tended to approach the model; however, this was the case in only one of the eagle trials that led to a collective response. In contrast, remaining in place may be a relatively effective strategy to avoid being taken by an eagle (Arlet and Isbell 2009). Yet we cannot rule out that these differences may be due to samangos perceiving a perched eagle as less dangerous than one flying overhead. While crowned eagles do drop down from dense canopy onto monkeys, samangos may not see these predators as often prior to an attack, which could explain this discrepancy.

Approaching a leopard, as we witnessed here, may help individuals avoid mortality as ambush predators are often less likely to continue a hunt if prey signals that they are aware of the present danger (Woodland et al. 1980; Adams and Kitchen 2018). This response may also deter a leopard from concealing itself nearby but may also be a more noticeable reaction to other group members unaware of potential danger, leading to more widespread responses. In some instances, alarm calling may solicit help for mobbing (Isbell 1994). While we did not observe mobbing or harassment behavior following approaches, this was potentially due to our time-limited trials. Given that leopard models were approached more often, increased alarming could have also functioned to recruit more group members to participate in this potentially costly behavior. We also observed that initial detectors often continued alarming long after both eagle and leopard models were removed, but this was generally not the case with the python model. This may indicate that once detected, snakes pose less risk than the other ambush predators. For example, Mielke et al. (2019) found that sooty mangabeys (*C. atys*) react mildly to stationary snakes or snake models, potentially indicating that, once detected, a nonmoving snake poses little risk.

Previous experiments with this population showed that samangos spend more time foraging on the ground while being observed by humans (Nowak et al. 2014). This is likely due to a "human-shield" effect where predators avoid contact with humans, and samangos take advantage of this increase in safety. Leopards may infrequently hunt samangos in this habitat compared with other available mammals (Williams et al. 2018), but it is uncertain where they are most frequently encountered on the landscape compared with eagles that are encountered more frequently (LaBarge et al. 2020a). From a prey animal's perspective, encounters with a potential predator should elicit a response (including freezing or other cryptic reactions) even if the predator itself is not engaged in an attack. Additionally, sit-and-wait terrestrial predators with relatively small hunting domains are expected to produce outsized risk effects in their prey (Schmitz 2007; Miller et al. 2014). It is possible here that our presence through general observation throughout the day would have led to relaxed risk perceptions prior to initiating trials. This could have led to delays in responses if most individuals are less reactive when humans are present. Conversely, if human presence produces relaxed perceptions of leopard risk across the landscape, this could lead to stronger responses if an unwary individual happens to encounter a predator while in a more vulnerable position. At minimum we have demonstrated here that observed encounter frequency does not necessarily track with the magnitude of antipredator response in this population of samangos.

Predator-primate interactions are difficult to observe because they are unpredictable, rapid, and relatively rare (Isbell 1994; Janson et al. 2014). Compounding this issue is that many unhabituated predators tend to avoid proximity to potentially dangerous humans (Ngoprasert et al. 2007; LaBarge et al. 2020b), minimizing the chances than an observer witnesses an encounter during data collection. Observational studies that look for correlations between antipredator behaviors and habitat- or location-specific risk often overlook the possibility that prey perceive themselves to be relatively safe while accompanied by an observer (Nowak et al. 2014). Field experiments can ameliorate this problem by allowing researchers to control when and where predator cues are used (Adams and Kitchen 2018; LaBarge et al. 2020b). Limitations to our study included the presence of an observer collecting behavioral data on our habituated subjects while we conducted these experiments. If subjects already perceived themselves to be relatively safe from certain predators while in proximity to humans, then this potential effect on perceived risk could have altered initial detection times. Nevertheless, these realistic reactions to visual models indicate that experiments are an effective means of simulating these encounters. Future studies with expanded numbers of groups should investigate whether the presence/absence of an observer influences detection time and overall probability of collective response. Finally, we could not test how group size might have limited or enhanced the probability of a collective response, but future studies using random slope models with many groups (> 10) of varying sizes could provide information on the importance of this trait for samango predator detection (Grueber et al. 2011). Studies that can further minimize the presence of observers or eliminate direct observation would be better positioned to investigate whether underlying spatial patterns of risk from various predators result in variation in detection time or overall response.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval We followed all animal research (IACUC) guidelines from The State University of New York as well as all applicable South African and international guidelines. We received research permission from the Limpopo Province Department of Economic Development and Tourism (Permit # ZA/LP/81996), University at Buffalo IACUC (#ANT07037N), and Durham University Animal Welfare Ethical Review Board.

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References

Adams DB, Kitchen DM (2018) Experimental evidence that titi and saki monkey alarm calls deter an ambush predator. Anim Behav 145: 141–147. https://doi.org/10.1016/j.anbehav.2018.09.010

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–266. https://doi.org/10.1163/156853974X00534

Arlet ME, Isbell LA (2009) Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. Behav Ecol Sociobiol 63:491–499. https://doi.org/10.1007/s00265-008-0682-5

Arnold K, Pohlner Y, Zuberbühler K (2008) A forest monkey's alarm call series to predator models. Behav Ecol Sociobiol 62:549–559. https://doi.org/10.1007/s00265-007-0479-y

Bednekoff PA, Lima SL (1998)Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. Proc R Soc Lond B 265:2021–2026. https://doi.org/10.1098/rspb.1998.0535

Brent LJN, Semple S, MacLarnon A, Ruiz-Lambides A, Gonzalez-Martinez J, Platt ML (2014) Personality traits in rhesus macaques (*Macaca mulatta*) are heritable but do not predict reproductive output. Int J Primatol 35:188–209. https://doi.org/10.1007/s10764-013-9724-6

Bürkner PC (2017) brms: an R package for Bayesian multilevel models using Stan. J Stat Softw 80:1–28. https://doi.org/10.18637/jss.v080.i01

Caro T (1995)Pursuit-deterrence revisited. Trends Ecol Evol 10:500–503

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago

Coleman BT, Hill RA (2014) Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. Anim Behav 88:165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Conradt L (2011) Collective behaviour: when it pays to share decisions. Nature 471:40–41

Coss RG, McCowan B, Ramakrishnan U (2007)Threat-related acoustical differences in alarm calls by wild bonnet macaques (*Macaca radiata*) elicited by python and leopard models. Ethology 113: 352–367. https://doi.org/10.1111/j.1439-0310.2007.01336.x

Couchoux C, Clermont J, Garant D, Réale D (2018) Signaler and receiver boldness influence response to alarm calls in eastern chipmunks. Behav Ecol 29:212–220. https://doi.org/10.1093/beheco/arx152

Cresswell W, Quinn JL (2010) Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. Anim Behav 80:643–648. https://doi.org/10.1016/j.anbehav.2010.06.024

Crockford C, Wittig RM, Mundry R, Zuberbühler K (2012) Wild chimpanzees inform ignorant group members of danger. Curr Biol 22: 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Fernández-Juricic E, Kacelnik A (2004) Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. Behav Ecol Sociobiol 55:502–511. https://doi.org/10.1007/s00265-003-0698-9

Fernández-Juricic E, Beauchamp G, Bastain B (2007)Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. Anim Behav 73:771–778. https://doi.org/10.1016/j.anbehav.2006.09.014

Forster JJ, McDonald JW, Smith PWF (2003) Markov chain Monte Carlo exact inference for binomial and multinomial logistic regression models. Stat Comput 13:169–177. https://doi.org/10.1023/A:1023212726863

Frechette JL, Sieving KE, Boinski S (2014) Social and personal information use by squirrel monkeys in assessing predation risk. Am J Primatol 76:956–966. https://doi.org/10.1002/ajp.22283

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hartig F (2016) DHARMa: residual diagnostics for hierarchical regression models, version 1.5, https://mran.microsoft.com/snapshot/2016-11-19/web/packages/DHARMa/vignettes/DHARMa.html

Hochman V, Kotler BP (2007) Patch use, apprehension, and vigilance behavior of Nubian ibex under perceived risk of predation. Behav Ecol 18:368–374. https://doi.org/10.1093/beheco/arl087

Isbell LA (1994) Predation on primates: ecological patterns and evolutionary consequences. Evol Anthropol 3:61–71. https://doi.org/10.1002/evan.1360030207

Isbell LA, Bidner LR (2016) Vervet monkey (*Chlorocebus pygerythrus*) alarm calls to leopards (*Panthera pardus*) function as a predator deterrent. Behaviour 153:591–606. https://doi.org/10.1163/1568539X-00003365

Isbell LA, Etting SF (2017) Scales drive detection, attention, and memory of snakes in wild vervet monkeys (*Chlorocebus pygerythrus*). Primates 58:121–129. https://doi.org/10.1007/s10329-016-0562-y

Isbell LA, Young TP (1993) Human presence reduces predation in a free-ranging vervet monkey population in Kenya. Anim Behav 45:1233–1235. https://doi.org/10.1006/anbe.1993.1145

Janson CH, Monzón J, Baldovino MC (2014) Experimental analysis of predator and prey detection abilities in rainforest: who has the advantage? Behaviour 151:1491–1512. https://doi.org/10.1163/1568539X-00003198

Kendal RL, Coolen I, Laland KN (2004) The role of conformity in foraging when personal and social information conflict. Behav Ecol 15:269–277. https://doi.org/10.1093/beheco/arh008

King AJ, Cowlishaw G (2007) When to use social information: the advantage of large group size in individual decision making. Biol Lett 3:137–139. https://doi.org/10.1098/rsbl.2007.0017

Kruschke J (2014) Doing Bayesian data analysis: a tutorial with R, JAGS, and Stan. Academic Press, London

LaBarge LR, Allan ATL, Berman CM, Margulis SW, Hill RA (2020a) Reactive and pre-emptive spatial cohesion in a social primate. Anim Behav 163:115–126. https://doi.org/10.1016/j.anbehav.2020.03.005

LaBarge LR, Hill RA, Berman CM, Margulis SW, Allan ATL (2020b) Anthropogenic influences on primate antipredator behavior and implications for research and conservation. Am J Primatol (published online). https://doi.org/10.1002/ajp.23087)

Lima SL (1995) Collective detection of predatory attack by social foragers: fraught with ambiguity? Anim Behav 50:1097–1108

Lima SL (1996) The influence of models on the interpretation of vigilance. MIT Press, Cambridge

Lüdecke D (2018) sjstats: statistical functions for regression models. R Packag version 014 0, https://cran.r-project.org/web/packages/sjstats/sjstats.pdf

Mielke A, Crockford C, Wittig RM (2019) Snake alarm calls as a public good in sooty mangabeys. Anim Behav 158:201–209. https://doi.org/10.1016/j.anbehav.2019.10.001

Miller JRB, Ament JM, Schmitz OJ (2014) Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. J Anim Ecol 83:214–222. https://doi.org/10.1111/1365-2656.12111

Moen EL, Fricano-Kugler CJ, Luikart BW, O'Malley AJ (2016) Analyzing clustered data: why and how to account for multiple observations nested within a study participant? PLoS One 11:e0146721. https://doi.org/10.1371/journal.pone.0146721

Ngoprasert D, Lynam AJ, Gale GA (2007) Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. Oryx 41:343–351. https://doi.org/10.1017/S0030605307001102

Nowak K, Le Roux A, Richards SA, Scheijen CPJ, Hill RA (2014) Human observers impact habituated samango monkeys' perceived landscape of fear. Behav Ecol 25:1199–1204. https://doi.org/10.1093/beheco/aru110

Pays O, Beauchamp G, Carter AJ, Goldizen AW (2013) Foraging in groups allows collective predator detection in a mammal species without alarm calls. Behav Ecol 24:1229–1236. https://doi.org/10.1093/beheco/art057

Pereira ME, Macedonia JM (1991) Ringtailed lemur anti-predator calls denote predator class, not response urgency. Anim Behav 41:543–544. https://doi.org/10.1016/S0003-3472(05)80861-9

Schmitz OJ (2007) Predator diversity and trophic interactions. Ecology 88:2415–2426. https://doi.org/10.1890/06-0937.1

Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim Behav 28:1070–1094. https://doi.org/10.1016/S0003-3472(80)80097-2

Shibasaki M, Kawai N (2009) Rapid detection of snakes by Japanese monkeys (*Macaca fuscata*): an evolutionarily predisposed visual system. J Comp Psychol 123:131–135. https://doi.org/10.1037/a0015095

Shultz S (2001) Notes on interactions between monkeys and African crowned eagles in Taï National Park, Ivory Coast. Folia Primatol 72:248–250. https://doi.org/10.1159/000049945

Shultz S, Thomsett S (2009) Interactions between African crowned eagles and their prey community. In: McGraw WS, Zuberbühler K, Noë R (eds) Monkeys of the tai forest: an African primate community. Cambridge University Press, Cambridge, pp 171–193

Treves A (1998) The influence of group size and neighbors on vigilance in two species of arboreal monkeys. Behaviour 135:453–481

van Schaik C, Mitrasetia T (1990) Changes in the behaviour of wild long-tailed macaques (*Macaca fascicularis*) after encounters with a model python. Folia Primatol 55:104–108

Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J (2008) Quorum decision-making facilitates information transfer in fish shoals. Proc Natl Acad Sci U S A 105:6948–6953. https://doi.org/10.1073/pnas.0710344105

Watson KK, Li D, Brent LJN, Gonzalez-Martinez J, Ruíz-Lambides AV, Robinson AG, Skene JHP, Platt ML (2015) Genetic influences on social attention in free-ranging rhesus macaques. Anim Behav 103:267–275. https://doi.org/10.1016/j.anbehav.2015.02.012

Whittingham MJ, Butler SJ, Quinn JL, Cresswell W (2004) The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. Oikos 106:377–385. https://doi.org/10.1111/j.0030-1299.2004.13132.x

Wich SA, Sterck EHM (2003) Possible audience effect in Thomas langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model. Am J Primatol 60:155–159. https://doi.org/10.1002/ajp.10102

Willems EP, Hill RA (2009)Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology 90:546–555. https://doi.org/10.1890/08-0765.1

Williams ST, Williams KS, Lewis BP, Hill RA (2017) Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. R Soc Open Sci 4:161090. https://doi.org/10.1098/rsos.161090

Williams KS, Williams ST, Fitzgerald LE, Sheppard EC, Hill RA (2018) Brown hyaena and leopard diets on private land in the Soutpansberg Mountains, South Africa. Afr J Ecol 56:1021–1027. https://doi.org/10.1111/aje.12539

Woodland DJ, Jaafar Z, Knight ML (1980) The "pursuit deterrent" function of alarm signals. Am Nat 115:748–753. https://doi.org/10.1086/283596

Zuberbühler K, Jenny D, Bshary R (1999) The predator deterrence function of primate alarm calls. Ethology 105:477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

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