Foraging under Predation Risk: A test of giving-up densities with samango monkeys in South Africa

SASSOON, RACHEL

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Foraging under Predation Risk: A test of giving-up densities with samango monkeys in South Africa

Rachel Sassoon
Department of Anthropology
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Abstract

Animals frequently make a trade-off between food and safety and will sacrifice feeding effort if it means safety from predators. A forager can also vary its vigilance levels to manage predation risk. Giving-up densities (GUDs), the amount of food items left once a forager has quit an experimental food patch, have been used extensively as measures of foraging behaviour under risk of predation in a wide range of species. Vigilance also serves as an anti-predatory response to predation risk and has been the focus of a range of behavioural studies. However, very few studies have looked at these two measures together.

The principal aim of this study was to determine the effect of habitat factors on the foraging behaviour of samango monkeys (*Cercopithcus mitis erythrarchus*) by measuring GUDs in artificial food patches and foraging behaviour, and relating this to height from the ground, canopy cover, habitat visibility and observed behaviour. The second objective was then to determine the extent to which the experimental approach matched observed behaviour in measuring primate responses to predation risk.

The monkeys revealed lower GUDs with increasing height and with decreasing canopy cover and but were not affected by habitat visibility. Vigilance varied considerably with only conspecific and observer vigilance showing significant effects. Conspecific vigilance increased with height and decreasing canopy cover. Vigilance directed at observers increased with decreasing canopy cover. There was no effect of habitat visibility on any of the component behaviours of vigilance.

The vigilance behaviour of the monkeys did not completely compliment the GUD results. The findings of this study confirm the prediction that habitat plays a key role in the foraging behaviour of samango monkeys but that vigilance is more sensitive to other factors such as sociality. Further work is required to determine the extent to which experimental approaches based on giving up densities match patterns of antipredatory behaviour recorded by observational methods.

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Chapter 1

Introduction

Predation is one of the most significant selective pressures on animals with direct effects leading to mortality. However, predators also indirectly affect their prey (Brown and Alkon, 1990; Lima, 1998). Non-lethal effects can influence the habitat choice (Creel et al. 2005; Hernandez and Laundre, 2005) and foraging behaviour of prey across a patchy environment by reducing activity times (Altendorf et al. 2001), increasing group size and changing vigilance levels (Childress and Lung, 2003). These non-lethal effects cause prey to trade food for safety (Brown and Kotler, 2004) by foraging in safer, less rewarding food patches or by increasing vigilance while foraging in riskier areas (Lima and Dill, 1990; Sih, 1980; Brown 1999). On a population level, the non-lethal effects of predation may be more important than the lethal effects (Kotler and Holt, 1989; Brown et al. 1992; Brown, 1999). Foraging theory addresses the question of how an animal searches for food items while not becoming food for its predators (Brown, 1992).

Understanding the spatial distribution of animals and understanding the factors that cause these distributions is essential to making predictions about how animals will respond to environmental change (Heithaus and Dill 2002). The spatial distribution of food and differences in habitat may be important in determining habitat use (Lima and Dill, 1990). Situations in which habitats with high food availability are also the most dangerous are of particular interest as the animal may have to trade-off food and safety. Predation is considered a significant selective force in shaping morphological and behavioural characteristics of animals (Lima and Dill, 1990). In the presence of predators, prey can alter their behaviour so that they are more difficult to catch, detect or encounter (Lima, 1998). Crypsis is one example in which predation risk may influence prey decision making (Lima and Dill, 1990). A cryptic species can ultimately avoid predators that rely on sight and movement to locate their prey as long as it remains motionless. However, it must move at some point in order to find both food and mates. There is a benefit and cost to both options. The animal cannot be cryptic and active simultaneously, thus resulting in a conflict to determine the extent to which one behaviour will be selected over the other. This conflict must be resolved based on the animal's assessment of the risk in its environment and the costs and benefits associated with the various behavioural responses. One of the best ways to demonstrate that animals balance safety against food acquisition is to deprive them of food. A hungry animal faces a risk of starvation and must feed at a higher rate in order to meet their energetic needs. Food-deprived animals would then be expected to accept an increase in predation risk for higher energy gains. A good example of this was found in dark-eyed juncos (*Junco hyemalis*) (Lima, 1988). Juncos with reduced energy reserves initiated feeding before individuals with normal reserves.

Group living can significantly affect the way animals balance the trade-off between risk and foraging (van Schaik, 1983). By living in groups, individuals can reduce their predation risk. On the other hand, solitary animals do not have this benefit and must effectively monitor their environment while maintaining foraging behaviour. Using a modelling approach across a number of primate species, Wrangham (1980) suggested that the main advantage to group living was resource defence. However, several studies have suggested that group living is actually an anitpredator strategy (Alexander, 1974). By living in a group, an individual can potentially reduce its predation risk and the amount of time it spends vigilant. This is done through two principal mechanisms, the dilution effect (Dehn, 1990), where increases in group size can reduce individual predation risk and detection effects (Pulliam, 1973; Lima, 1995), where the larger the group, the more potentially vigilant animals and the higher the chance of identifying a predator. Individuals can therefore reduce their own vigilance, thus maintaining a higher foraging efficiency. Also, the detection effect could allow the group to forage in areas perceived to be of high predation risk. The disadvantage to this is that larger groups themselves may attract predators and other individual costs, such as mate competition and feeding competition (Stanford, 2002). Trade-offs between food and safety are known to influence the size of animal groups. In general, the formation of large groups can reduce the risk of predation but intraspecific competition selects for smaller sizes (Janson and Goldsmith; Hill and Lee, 1998).

The risk of predation can vary with environmental factors. These include vegetation and the degree of cover it can provide or the accessibility of a predator to certain areas (Hochman and Kotler, 2004). With such variation, animals will be forced to vary their foraging behaviour accordingly across habitats. Cowlishaw (1997) explored the balance between foraging and predation risk from leopards (*Panthera pardus*) and lions (*Panthera leo*) and the effects that this can have on habitat use in chacma baboons (*Papio cynocephalus ursinus*) in Namibia. The baboons were choosing to forage in low risk poor-food habitats, rather than the high risk food-rich habitats. This was also found in a population of chacma baboons in De Hoop, South Africa (Hill, 1999) and in vervet monkeys (*Cercopithecus aethiops*) (Willems and Hill, 2009) where the group was actively avoiding areas with high perceived baboon and leopard risk. These results show that predation risk is a significant force in shaping the foraging behaviour of these populations, that antipredator behaviour is not fixed and that individuals have different behavioural responses depending on the extent of risk (Hill and Cowlishaw, 2002). An example being that baboons living in small, high risk groups use refuges such as tall trees and cliff faces more than larger groups.

In a heterogeneous environment, an animal must choose where to forage among a variety of habitats or patches. Patches are subsets of the environment that often yield higher energy gains or benefits than the environment as a whole (Brown, 1988). Once a habitat patch has been chosen for harvesting, an animal must decide when and where to eat, but also, how much time and effort it should devote to a food patch (Brown, 1988; Lima and Dill, 1990; Brown, 2000). A forager can vary the total, average, marginal or net return from a patch by varying the foraging time spent at each patch (Brown, 1988). The marginal value theorem for patch use states that a forager should continue foraging in a depletable food patch until the harvest rate from that patch no longer exceeds the average harvest rate generated from travelling to and exploiting another patch (Charnov, 1976). The marginal theorem applies when the forager can accurately assess the quality of the present patch, has knowledge of the environment as a whole and the distribution of patch qualities, does not deplete the quality of the environment and its objective is to maximise harvest rate. However, these assumptions are restrictive (Brown, 1988). Foraging will affect energy gain but will also affect other aspects of fitness such as predation risk. Animals will not just forage but will engage in other fitness-determining behaviours such as resting, grooming and territorial defense. Foraging activity may not only decrease the resources of a specific patch but also, could reduce the resources of the whole environment.

The restrictions of optimal patch use behaviour by a forager can be simplified to consider predation risk, situations where the forager can engage in other fitness enhancing activities and may experience reduction in the quality of the environment during a foraging period (Gilliam and Fraser, 1987; Brown, 1988). The goal of the forager is to distribute its time between foraging and alternative activities in order to maximise fitness. Most models can be translated into a simple rule for patch departure (Brown, 2000). The patch should be exploited until the marginal cost of foraging equals the marginal benefits of exploitation (Brown, 1988; 1992). For a forager in a risky environment this occurs when $H = C + P +$

MOC. A food patch should be left when the benefits of the harvest rate, H, no longer exceeds the sum of the energetic, C, predation, P, and missed opportunity costs of foraging, MOC (Brown, 1988, 1992). The last cost arises from not being able to forage elsewhere or engage in other fitness enhancing activities while at the patch. Predation cost is probably the most significant cost to foraging behaviour (Brown, 2000). Often it can be very large. For gerbils in Israel, the predation costs can be up to 8-10 times higher than the metabolic costs (Brown, 2000).

If harvest rate is a function of patch type and resource density, giving-up densities (GUDs) can be used to describe the quitting harvest rate (Brown, 1988). The GUD is the amount of food left in a depletable food patch after a forager has finished harvesting the patch (Brown, 1988). The use of artificial or manipulated food patches offers two main advantages (Brown, 1988). First, the foragers remain in their natural environment and are still exposed to competition and predation risks. Second, this experimental setup allows for the manipulation of specific variables while others are held constant. By controlling for metabolic and missed opportunity costs of foraging, GUDs can be used to measure the changes in the foraging costs of predation. To validate the model, all four components can be tested. To test for the effect of harvest rate, H on GUDs requires holding C, P and MOC constant. Adjacent artificial food patches in the same microhabitat should not differ in C, P or MOC. Therefore, GUDs which differ in substrate should reflect variations in harvest rates. To test for the effect of energetic costs, C on GUDs requires holding H, P and MOC constant. When ambient temperatures are below the forager’s ‘thermal neutral zone’, the metabolic costs of foraging should be influenced by temperature. Adjacent patches with the same substrate should not differ in H, P or MOC. Increasing P by manipulating predation risk should result in an increase in GUDs. Increasing the MOC by providing different resources or foraging opportunities should also increase GUDs. By manipulating patches in ways which are known to increase harvest rate, foraging costs, missed opportunity costs and predation risk, one can test whether the behaviour of the forager is consistent. The model can also be used to manipulate the forager to reveal its preferences and how it measures the environment. Temporal or spatial differences in the GUDs of a forager represent the effects of alternative habitats on missed opportunity costs, harvest rates foraging cost and predation risk. Species and habitat differences can be measured in any of these costs by holding other costs constant across habitats. Missed opportunity costs can be controlled for by making sure that several patches are accessible to the same forager. If the distance between these patches is relatively short, then while foraging either patch the forager experiences the same set of differing activities and therefore, experiences the same missed opportunity cost in each patch. Harvest rates can be controlled by making sure that the structure of the patches is the same in terms of the factors that affect harvest rate. These include substrate and resource type.

The first step is to develop a suitable food patch with diminishing returns for the study species. Experimentally, GUDs have been measured by making a depletable food patch in which food is mixed thoroughly into a non-edible substrate, in a tray or a tub, using the tray or the tub as the artificial resource patch (Brown, 1988). A small amount of food is used and a large amount of substrate to create the diminishing returns. As the forager harvests the patch, each piece of food will be harder to find than the last. The food must be rich enough to attract and keep the forager at the patch. Yet, the amount of food must be small enough that the animal does not become satiated. The balance between amount of food items and volume of substrate must be correct as the diminishing returns are to cause the forager to leave the patch before all the food items have been harvested (Emerson et al, 2011). The substrate increases search time and encourages diminishing returns. The artificial food patch gives the GUD for the most efficient forager. Often this is the last forager to have harvested thoroughly from the patch. If less efficient foragers visit later, they will not gain any rewards from exploiting the patch. However, if a more efficient forager visits the patch later, it will gain reward from harvesting the patch. The GUD as the animal leaves the patch is a measure of its foraging costs. Therefore, the patch is insensitive to the number of foragers that visit.

In order to reduce predation risk, animals will often sacrifice feeding effort (Sih, 1980; Lima and Dill, 1990; Kotler et al, 1994). Given the choice between a risky patch with high energetic returns and a safe patch with lower returns, a forager may not choose to maximise its energy gain or resource acquisition and may choose a lower rate of gain if such circumstances mean greater safety from predators. In order to take greater risks, greater benefits must be on offer (Brown and Kotler, 2004). In safer habitats, resources and foraging opportunities are more fully depleted and the opposite is found in the more risky habitats (Hugie and Dill, 1994). Under increased predation risk, foragers will often direct their efforts to safer patches and food will be depleted from these patches first (Brown et al, 1988; Jacob and Brown, 2000; Hochman and Kotler, 2006). If risk increases, less time should be devoted to foraging and the forager should leave the patch, either to find another patch or to engage in other fitness enhancing activities (Brown, 1999).

Many habitats are heterogeneous (Abu Baker and Brown, 2010) and risk will vary over space and time. Risky and safe habitats or time of day results in spatial and temporal variation in risk and can produce an animal's 'landscape of fear' (Laundre et al, 2001). As prey animals move about the physical environment, they are constantly changing their foraging behaviour in response to varying levels of predation risk. It can be said that such animals inhabit in a second landscape, one with changing levels of risk or fear. This is known as an animal's landscape of fear (Laundre et al, 2001). The 'peaks' and 'valleys' of this landscape represent the changes in predation risk for the prey animal and its' fear. The general landscape is influenced by the specific predator and encounter rate with predators, lethality of predators and vigilance levels (Brown et al, 1999; Laundre et al, 2010).

Risky areas can refer to riskier habitats such cover versus open areas or being on the edge of a habitat periphery of a group. When offered food patches with equal opportunity, foragers should leave riskier areas at a higher GUD (Brown, 1988). Feeding activity is often biased toward safer habitats with higher GUDs found in riskier habitats (Lima, 1988; Brown and Kotler, 2004). Ungulates have higher GUDs in forests and at forest edges and lower GUDs in open habitats (Altendorf et al, 2001). On the other hand, rodents and birds perceive a higher predation risk in the open habitats (higher GUDs) and prefer to forage from food patches that provide cover (lower GUDs) (Kotler et al, 1991; Jacob and Brown, 2000; Oyugi and Brown, 2003).

The majority of primate species have predator alarm calls and many species have predator-specific vocalisations (Seyfath et al, 1980; Zuberbuhler et al, 1997). These alarm calls can be used to measure spatially perceived predation risk. Each alarm call is acoustically different depending on the predator threat and initiates a different behavioural response. In one of the first studies to produce a behavioural landscape of fear, Willems and Hill (2009) recorded the location of predator-specific vervet alarm calls within their home range to produce predator-specific landscapes of fear. They found that chacma baboon (*Papio ursinus*) and leopards (*Panthera pardus*) to be the main predators of this population and that the monkeys avoided areas where predation risk was perceived to be high. Eagle and snake had no effect on the monkeys' ranging behaviour. The effect of baboons and leopards was stronger than the effect of food availability. The lack of an eagle effect was attributed to the fact that eagles have such large ranges, can be detected early and at a distance and the effective response is to move vertically down to find cover, rather than move horizontally across the habitat. The lack of a snake effect was attributed to the fact that snakes are not significant predators of vervets. Despite this, this study provides strong evidence for spatial variation in predation risk as a major force affecting primate behaviour.

Animals can gain safety through vigilance and apprehension but at a foraging cost (Brown, 1999; Kotler et al, 2010). Vigilance is defined as time spent scanning surroundings with the head up (Hochman and Kotler, 2006). An animal cannot forage and scan the environment at the same time (Lima, 1998). Therefore, animals often have to make a trade-off between time spent foraging and time spent being vigilant. In response to perceptions of a predator's location, prey must select an optimal level of vigilance (Brown et al, 1999). Even in the absence of an impending attack, prey should maintain a baseline level of apprehension just in case there is the possibility of attack. If the level of apprehension is set too high, valuable feeding opportunities will be missed. However, if apprehension is set too low, the likelihood of being killed by the predator increases. This is another trade-off that foragers make; safety against resource acquisition. The baseline level of apprehension is set in response to the number, the state and the feeding rate of the prey, but also, the abundance and characteristics of the predator. In terms of the predator, this level of apprehension can determine the catchability of prey and the quality of a prey patch (Brown et al, 1999). When prey is abundant or predators are rare, prey should lose their apprehension.

A number of studies have analysed vigilance as a behavioural response to predation risk in ungulates. Nubian ibex (*Capra nubiana*) are more apprehensive and therefore, had higher vigilance levels at greater distances from cliff refuges (Hochman and Kotler, 2006), mule deer (*Odocoileus hemionus*) had higher vigilance behaviour at patch edges when in open microhabitats or forest interiors (Altendorf et al., 2001) and elk (*Cervus elaphus*) and bison (*Bison bison*) of Yellowstone National Park showed increased vigilance after the reintroduction of wolves (*Canis lupis*) (Laundre et al, 2001).

Giving-up density experiments have been employed in a number of studies, across a variety of taxa including rodents (Jacob and Brown, 2000; van der Merwe and Brown, 2008; Kotler et al, 2010), birds (Lima, 1988; Olssen et al, 2002; Oyugi and Brown, 2003) lagomorphs (Morris, 2005; Abu Baker and Brown, 2009) and ungulates (Altendorf et al, 2001; Hochman and Kotler, 2006; Shrader et al, 2008; Rieucau et al, 2009). However, the use of GUDs is fairly new to primate research and includes studies on samango monkeys (Emerson et al, 2011; Emerson and Brown, 2012), thick-tailed bushbabies, *Otolemur crassicaudatus*, (McArthur et al, 2012), vervet monkeys, *Chlorocebus aethiops* (Makin et al, 2012) and blue *Cercopithecus mitis* and redtailed monkeys *Cercopithecus ascanius* (Houle et al, 2006). Arboreal primates are an interesting study group as predation risk can be measured vertically and extended up into the canopy.

Aims of the Study

The primary focus of this thesis is to measure predation risk in samango monkeys combining experimental and behavioural approaches. The study has two main objectives:

1. To replicate and expand the work by Emerson et al (2011) in a different habitat and in close proximity to a crowned eagle nest
2. Validate and examine the relationship between GUDs and vigilance behaviour to determine if observed behaviour matches GUDs

Chapter 2

Study Site and Study Species

STUDY SITE

The study was conducted from February to July 2012 at the Lajuma Environmental Research Centre (4.3 km^2), located in the western Soutpansberg Mountain Range, Limpopo Province, South Africa (29^{o}26’E, 23^{o}01’S; Figure 2.1). Due to its high biotic diversity, Lajuma was declared a Natural Heritage Site in 1997. It also forms part of the Thavha Ya Muno Private Nature Reserve (50km^2), the Soutpansberg Conservancy and the UNESCO Vhembe Biosphere Reserve. This reserve covers an area of 30,701km^2 from the borders of Botswana, Zimbabwe and Mozambique borders, to the Kruger National Park area, and just south of the Blouberg and Soutpansberg mountain ranges. The Soutpansberg mountain range covers an area of approximately 6800 km^2 from the Blouberg mountain in the west to Kruger National Park in the east. Altitude ranges from 250 m above sea level to 1748 m, its highest peak ‘Letjume’, located on the western half of the Soutpansberg range and is characterised by steep southern slopes and moderate northern slopes (Mostert et al. 2008). Major soil types in the area include quartzite and rich clay soils derived from basalt and diabase dykes that are prone to erosion along the southern slope. Also, acidic sandy soils derived from weathered sandstone, fine-grained deep sands derived from the Aeolian Kalahari sands and peat soils that occur along the cooler high wetlands (Mostert et al. 2008).

There are three specific climatic regions in the Soutpansberg range. On the southern and eastern slopes of the higher peaks, the climate is humid, in the south it is sub humid and in the north it is semi arid (Berger et al. 2003). The Soutpansberg experiences orographic rainfall due to its east-west orientation. This is due to moisture-rich air from the Indian Ocean that is driven by the south-easterly winds into the steep slopes of the southern Soutpansberg (Kabanda, 2003) and results in large amounts of rain falling on these slopes. This high rainfall then creates a rain-shadow effect along the northern slopes of the Soutpansberg. The climate varies considerably due to the high topographic diversity and changes in altitude over short distances (Mostert et al. 2008). Two main seasons exist in the Soutpansberg. A cool, dry season from May to August with temperatures ranging from 12 to 22 °C and a warm, wet season from December to February with temperatures ranging from 16 to 40 °C (Kabanda, 2003).

The flora of the Soutpansberg is highly diverse and contains 2693 plant species, with 594 tree taxa, including 24 endemics representing 1066 genera and 240 families (Hahn, 2006). Lajuma itself offers a diversity of vegetation types with montane grassland being found in the higher parts of the mountain. South facing ridges support evergreen forests. Further down the slopes, these evergreen forests are replaced with semi-deciduous woodland, thicket and riverine forest. (Hahn, 2006). These tall evergreen forests occur in natural fragments among the shorter woodlands and secondary short forest resulting from agricultural disturbance (Hahn, 2006). The micro-habitats of the Soutpansberg mountain range are home to a high diversity of animal communities. Thirty six percent of all known reptile species, 56% of bird species and 60% of all mammal species found in South Africa have been recorded here (Berger et al. 2003) with 145 species of mammals occurring in the Soutpansberg (Gaigher and Stuart 2003). Large carnivore species found in the mountain range are leopards, brown hyaenas (*Hyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*) (Gaigher and Stuart 2003). All five non-human primates are found at Lajuma: the chacma baboon (*Papio cynocephalus ursinus*), samango monkey (*Cercopithecus mitis erythracus*), vervet monkey (*Cercopithecus aethiops)* thick tailed bush baby (*Otolemur crassicaudatus)* and the southern lesser bushbaby *(Galago moholi).* Crowned eagle *(Stephanoaetus coronatus*), African black eagle (*Aquila verreauxii*) and the African rock python (*Python sebae*) also reside at Lajuma and could be potential predators of samango monkeys.

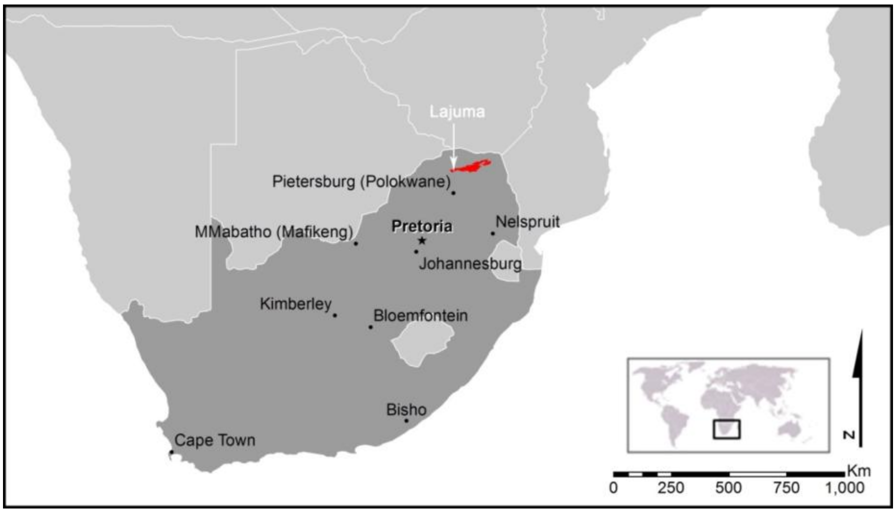

Figure 2.1 Map of South Africa showing the location of the Soutpansberg mountains (red) and the Lajuma Research Centre (Willems, 2007).

STUDY SPECIES

The samango monkey has an uncertain taxonomic status as it is termed *Cercopithecus mitis and Cercopithecus albogularis* (Skinner and Chimimba 2005; Kingdon et al, 2008). *C. albogularis* has two subspecies whereas *C. mitis* has seventeen. Despite this, on the IUCN Red List, *C. mitis* is listed as ‘Least Concern’ and not a priority for conservation efforts (Kingdon et al, 2008). However, when each sub-species is considered separately, one is grouped as ‘near threatened’, one as ‘endangered’, two are ‘critically endangered’, another two are considered ‘data deficient’, three are classed as ‘vulnerable’ and the remaining eight are ‘least concern’. In order to successfully conserve these monkeys, the taxonomic status must be known.

Samango monkeys are typical arboreal guenons and frequently live in large single-male multi-female troops of up to 40 individuals (Henzi and Lawes, 1987; Kaplin et al, 1998; Butynski, 1990; Cords, 2002a). While, it is not uncommon to observe troops with more than one resident male, especially during the breeding season (Cords, 2002a; Pazol, 2003), some large troops have multiple males all year round (Aldrich-Blake, 1970). Young males stay with the troop until about a year before they attain sexual maturity at approximately 6 years of age. They then leave and forage solitarily or join a smaller group of bachelor males (Henzi and Lawes, 1987). Females do not migrate and remain in their matrilineal troop.

The geographical range of *Cercopithecus mitis* occurs throughout central and eastern Africa; from Ethiopia in the north to Angola in the west and down into South Africa. Their distribution is patchy and is restricted to forest habitats in these areas (Estes, 1999; Skinner and Chimimba, 2005; Kingdon et al, 2008). Habitat fragmentation has resulted in small, geographically isolated populations of these monkeys with deforestation being a significant threat to such populations (Kingdon et al, 2008). The Soutpansberg contains one such population. At Lajuma, the samango monkeys’ home range encompasses the evergreen forests, the semi-deciduous woodlands and the riverine forest, as well as the disturbed secondary short forest (Heikamp, 2008).

The diet of samango monkeys is primarily frugivorous, with fruit consisting of 50 % of the diet (Lawes, 1991; Kaplin et al, 1998). However, leaves can constitute 26 % of the diet (Lawes, 1991) and insects can make up 25 % (Kaplin et al, 1998). Flowers, seeds and buds ar also eaten (Lawes, 1991; Kaplin et al, 1998). Samango monkeys are opportunistic and will eat insects when encountered (Skinner and Chimimba, 2005; Heikamp, 2008). Samango monkeys are at risk of predation from leopards (*Panthera pardus*), crowned eagles (*Stephanoaetus coronatus*) and black eagles (*Aquila verreauxii*) which all reside at Lajuma.

STUDY GROUP

The study population was a habituated group numbered at approximately 40 individuals at the time of the study (Coleman, 2013). Their home range is adjacent to and partly overlaps a larger troop of approximately 50 individuals with the sleeping trees of one core area bordering the other. For data collection, monkeys were not required to be individually identified. Nonetheless, preliminary work began in order to differentiate between age/sex classes. This can be difficult due to low habitat visibility. The adult male was easily distinguishable due to his large body size, presence of scrotum and comparatively long canines. Adult females are smaller with mammary glands. Subadults are typically smaller than females, juveniles are even smaller and generally inquisitive. Infants are easily identified due to their dependence on their mother. Identifying the sex of subadults was not possible due to the absence of mammary glands.

Chapter 3

Habitat characteristics and patch use in samango monkeys

INTRODUCTION

Predators affect their prey in two ways. The obvious impact is the direct killing of prey (lethal effect). But there is strong evidence to support the claim that predators have non-lethal impacts (Brown and Alkon, 1990; Brown, 1992). Prey should maintain a baseline level of apprehension just in case there is the possibility of attack (Brown et al, 1999). Many habitats are heterogeneous (Abu Baker and Brown, 2010) and risk will vary over space and time with spatial and temporal variation in risk producing an animal's landscape of fear (Laundre et al, 2001). Foraging theory predicts that in order to reduce predation risk, animals will sacrifice feeding effort (Sih, 1980; Lima and Dill, 1990; Kotler et al, 1994). They do so in two ways: (1) by reducing their time spent foraging and/or (2) increasing vigilance while foraging in riskier areas (Brown 1999). Put another way, animals must assess a foraging cost of predation to balance for the risk of predation.

Risky areas can refer to riskier habitats or being on the periphery of a group. As prey animals move about the physical environment, they are constantly changing their behaviour in response to varying levels of predation risk. It can be said that such animals inhabit in a second landscape, one with changing levels of risk or fear. This is known as an animal's landscape of fear (Laundre et al, 2001). The 'peaks' and 'valleys' of this landscape represent the changes in predation risk for the prey animal and its' fear. The general landscape is influenced by the specific predator and encounter rate with predators, lethality of predators and vigilance levels (Brown et al, 1999; Laundre et al, 2010). When animals are in areas that they perceive to have high predation risk, they respond with increased vigilance (Laundre et al, 2001). Therefore, the constant movement within a heterogeneous habitat results in varying levels of predation risk and respond by changing their vigilance levels.

A number of studies have analysed vigilance as a behavioural response to predation risk in ungulates. Nubian ibex (*Capra nubiana*) are more apprehensive and therefore, had higher vigilance levels at greater distances from cliff refuges (Hochman and Kotler, 2006), mule deer (*Odocoileus hemionus*) had higher vigilance behaviour at patch edges when in open microhabitats or forest interiors (Altendorf et al., 2001) and elk (*Cervus elaphus*) and bison (*Bison bison*) of Yellowstone National Park showed increased vigilance after the reintroduction of wolves (*Canis lupis*) (Laundre et al., 2001). Changes can also be attributed to different types of habitats and terrain (Laundre et al, 2010). Studies measuring landscapes of fear include ungulates (Shrader et al, 2008), rodents (van der Merwe and Brown, 2008) and primates (Willems and Hill, 2009; Coleman, 2013).

A forager can vary the total, average, marginal or net return from a patch by varying the foraging time spent at each patch. The patch should be exploited until the marginal cost of foraging equals the marginal benefits of exploitation (Brown, 1988). For a forager in a risky environment this occurs when $H = C + P + MOC$. A food patch should be left when the benefits of the harvest rate, H, no longer exceeds the sum of the energetic, C, predation, P, and missed opportunity costs of foraging, MOC (Brown, 1988). The GUD is the amount of food left in a depletable food patch after a forager has finished harvesting the patch (Brown, 1988).

When offered food patches with equal opportunity, foragers should leave riskier areas at a higher GUD (Brown, 1988). Feeding activity is often biased toward safer habitats with higher GUDs found in riskier habitats (Lima, 1988; Brown and Kotler, 2004). Different species have different perceptions about what constitutes a risky and safe patch. Ungulates have higher GUDs in forests and at forest edges and lower GUDs in open habitats (Altendorf et al, 2001). On the other hand, rodents and birds perceive a higher predation risk in the open habitats (higher GUDs) and prefer to forage from food patches that provide cover (lower GUDs) (Kotler et al, 1991; Jacob and Brown, 2000; Oyugi and Brown, 2003). Lima (1988) found that dark-eyed juncos (*Junco hyemalis*) only fed in dim light when there was adequate cover to forage.

GUDs have been employed to measure predation risk in samango monkeys. Emerson et al (2011) used experimental food patches at differing heights in trees to test the effects of habitat factors on the monkeys' predation risk. Arboreal monkeys are good subjects for such a study as they inhabit a complex, three-dimensional network (Treves, 2002). This complex habitat contains multiple refuges, sources of cover and escape routes. Typically, some refuges are inaccessible to a predator. For example, raptors that are large enough to kill a monkey are frequently too large to attack a monkey near the trunk of a tree (Overdorff et al, 2002). Due to the arboreal nature of samango monkeys, it is likely that they will spend much time foraging in higher forest strata. This has been recorded in a number of arboreal species. Patas monkeys spend more time in tall microhabitats compared with shorter microhabitats (Enstam and Isbell, 2004). Thomas langurs prefer to be in the higher strata as there is an increased risk of predation in the lower strata (0 to 10 m). Captive red-bellied and saddle-back tamarins have a preference for boxes higher off the ground when compared with lower boxes.

In addition to providing refuges, the arboreal environment can pose a visual challenge for predators and prey. If vegetation is dense, predators and prey can pass each other unnoticed (Treves, 2002). Cords (1990) demonstrated that wild redtail monkeys and blue monkeys decreased vigilance when surrounded by dense foliage. Vegetation can provide protective cover for prey but it can also limit effective monitoring of the environment. In this case, predators can go undetected. On the other hand, reduced vegetation and high visibility can result in a reduction in vigilance. Enstam and Isbell (2002) found that vervet monkeys reduced vigilance in more open areas, with Jaffe and Isbell (2009) reporting the same result.

Many eagles are surprise hunters (Noe and Bshuary, 1997). The preferred hunting method is to perch high up in the canopy, employing a sit-and-wait strategy that relies on ambushing and surprising their prey (Shultz, 2001; McGraw and Zuberbuhler, 2008). Ambush attacks rely on closed or broken canopy forest cover. However, a continuous canopy forest cover can be dangerous too as these predators can be difficult to detect (Boinski et al, 2003). Nonetheless, primates should avoid open, exposed areas with very little vegetative cover (Shultz, 2001) and seek out areas that provide adequate canopy cover.

A landscape of fear has been quantified for samango monkeys at Lajuma. Expanding upon the methods used by Willems and Hill (2009), Coleman (2013) measured predation risk and mapped the landscape of fear in the same population as the present study. Like vervet monkeys, samango monkeys also have distinct alarm calls that can be easily recognised by human observers (Cordeiro, 2003; Papworth et al, 2008). Coleman (2013) predicted that the monkeys would avoid areas with high perceived eagle and leopard predation risk. During the study, the only predator-specific alarm call heard was the eagle alarm call, identified as a series of ‘kas’ or ‘ka-trains’ by the adult male. There were no leopard-specific alarm calls. Perceived eagle predation risk was one of the most important factors affecting space use in this population. It had a strong negative association, suggesting that the monkeys perceived eagles to be such a serious threat that they avoided areas they considered high risk. The effect was stronger than any of the environmental factors measured, including food availability, which had no observed effect on samango space use. The two highest areas for perceived eagle risk were close to two known nesting sites; one for a crowned eagle pair and the other, a black eagle pair. This suggests a strong spatial variation in eagle predation risk throughout the monkeys' home range. It can be predicted that distance to eagle nest would influence perceived predation risk in these monkeys.

I applied the GUD technique (Brown, 1988) using artificial food patches to a population of free-living samango monkeys in the western Soutpansberg Mountains of South Africa to examine the effects of predation risk on foraging behaviour. The present study is an extension of earlier work by Emerson et al (2011) that employed GUDs to measure the effect of habitat characteristics (distance from the ground, blocked sightlines and proximity to trees and shrubs) on the foraging behaviour of samango monkeys. Their study found significant effects for height and sightlines, with lower GUDs with increasing height from the ground and higher GUDs when sightlines were blocked. No significant effect of distance to vegetation on GUDs was found. I followed their methods and applied them to the present study on the same troop of samango monkeys, but extended their approach by conducting the study in an area of high predation risk that also integrated distance from eagle nest. I also measured the canopy cover and habitat visibility of the study habitat to examine the effects of vegetative characteristics on foraging behaviour in more detail. The present study ran from early April until late July, with one experimental array set up in an area of tall evergreen forest (compared to the upland scrub forest of Emerson et al (2011)). The main aim of the present study was to confirm the height effect found by Emerson et al (2011) and expand upon their vegetative methods to determine the extent to which canopy cover and visibility affect predation risk in this population of samango monkeys.

Because samango monkeys are a predominantly arboreal species and this population perceive the greatest predation risk from aerial predators (Coleman, 2013), I made the following predictions:

1. lower GUDs with increasing height in trees
2. lower GUDs with increasing canopy cover
3. lower GUDs with good habitat visibility and clear sightlines
4. higher GUDs with decreasing distance to eagle nest

METHODS

Study Site

The research was conducted at the Lajuma Research Centre in the Soutpansberg Mountains, Limpopo Province, South Africa (29^{o}26E, 23^{o}01 S). The flora of the Soutpansberg is highly diverse (Hahn, 2006) and Lajuma itself is characterised by a diversity of habitats including tall evergreen forest, semi-deciduous woodland, thicket, riverine forest and grassland. Samango monkeys range from eastern and central Africa to Southern Africa where they occur in a variety of evergreen forests. Habitat fragmentation has resulted in small, geographically isolated populations of these monkeys and the Soutpansberg Mountains contain one such population. At Lajuma, the samango monkeys' home range encompasses the evergreen forests, the semi-deciduous woodlands and the riverine forest, as well as the disturbed secondary short forest (Heikamp, 2008). Their diet is primarily frugivorous, along with leaves, flowers and buds but they are opportunistic and will eat insects when encountered (Heikamp, 2008). Samango monkeys are at risk from leopards (*Panthera pardus*), crowned eagles (*Stephanoaetus coronatus*) and black eagles (*Aquila verreauxii*) which all reside at Lajuma.

Data Collection

The GUD Technique

Experimentally, GUDs have been measured by making a depletable food patch in which food is mixed thoroughly into a non-edible substrate in a tray or a tub, using the tray or the tub as the artificial resource patch (Brown, 1988). A small amount of food is used and a large amount of substrate to create the diminishing returns. As the forager harvests the patch, each piece of food must be harder to find than the last. The food must be rich enough to attract and keep the forager at the patch. Yet, the amount of food must be small enough that the animal does not become satiated. The balance between amount of food items and volume of substrate must be correct such that the diminishing returns cause the forager to leave the patch before all the food items have been harvested (Emerson et al, 2011). The substrate increases search time and encourages diminishing returns. The artificial food patch gives the GUD for the most efficient forager. Often this is the last forager to have harvested thoroughly from the patch. If less efficient foragers visit later, they will not gain any rewards from exploiting the patch. However, if a more efficient forager visits the patch later, it will gain reward from harvesting the patch. The GUD as the animal leaves the patch is a measure of its foraging costs. Therefore, the patch is insensitive to the number of foragers that visit.

Depletable food patches, yielding giving-up densities were used to measure the foraging costs of predation in samango monkeys. Methods employed to measure GUDs follow Emerson et al (2011). Artificial food patches were generated by thoroughly mixing 25 raw, dry peanut halves with 4 litres of untreated eucalyptus sawdust in plastic tubs (15 cm high, 45 cm diameter). A hole was put in the middle of the sawdust to show the difference to observers between an undisturbed patch (Figure 3.1) and a disturbed patch (Figure 3.2). To test the effect of increasing height on GUDs, food patches were hung at heights of 0.1 m, 2 m and 5 m from the ground in 12 trees (Figure 3.3), approximately 20 m apart, in a 3 x 4 grid in an area of tall evergreen forest. Patches were baited at 0930 hours and sieved at 1600 hours, where the remaining peanut halves were counted. Patches were prepared in late morning to allow for the troop to move off from the sleeping site. Often, patches were visited by several monkeys. Peanuts were never found on the ground but on occasions, sawdust was spilled from the tubs. If spilled sawdust was 1 litre or more, the datum from that food patch was excluded from the analysis. Whenever extensive spillage occurred, the sawdust was restocked back to 4 litres the following day prior to data collection. Regardless of extensive spillage, every few days the tubs were restocked with sawdust to maintain the correct volume due to continual foraging, wind and sieving. Patches were sieved every day, even if the monkeys had not visited. The experiments were run from 11th of April 2012 until 15th of July 2012 and resulted in 24 successful visits by the monkeys.

Figure 3.1. Undisturbed food patch with hole in the middle of the substrate.

Figure 3.2. A disturbed food patch showing that monkeys had been the foragers.

Figure 3.3. Artificial food patches hung at 0.1 m, 2 m and 5 m from the ground.

The foraging station, rather than individual foragers was the unit of replication in this study. GUDs are insensitive to the number of foragers and typically correspond to the last forager that visited (Hochman and Kotler, 2006). Lajuma has two habituated troops of samango monkeys that have adjacent home ranges. The location of the experimental array was in the core area of one of the troops' home range (Barn Group) and covered an area of 2400 m^2. The habitat was an area of tall evergreen forest with tree heights of up to 20 m (Hahn, 2006). This contrasts with Emerson et al (2011). Their study habitat was an area of upland scrub forest with a mean canopy height of 7 m. Within the experimental array was a crowned eagles' nest located on the periphery of the grid, between two stations. That part of the forest was near to the cliffs where raptors were often observed flying just above the canopy (R. Sassoon, pers. obs). During the study, the nest was not in use. However, despite this, it was predicted that the location of the nest would provide a novel element to the study.

Vegetation Characteristics: Exposed Skyline and Habitat Visibility

Blocked sightlines are known to increase GUDs in this troop (Emerson *et al*, 2011), showing that visibility is important when these monkeys make foraging decisions. For an arboreal species like the samango monkey, with aerial predators being a significant threat, and the main threat in this population (Coleman, 2013), one can assume that canopy cover also plays a key role in the monkeys' choice of where to forage . Measurements of habitat visibility and canopy cover were taken to determine the effects on GUDs.

To measure habitat visibility at each station, the starting point was directly underneath the patches. Measurements were then taken at the four cardinal compass directions (N, S, E and W) at distances of 5 m and 10 m away. A 75 cm x 75 cm board marked out as a 5 cm checkerboard is placed at heights 0 m and 2 m at both distances. A photograph was taken from the focal tree, at the same height as the checkerboard. For each distance, there were two photographs; one at the ground level and one at a height of 2 m; resulting in a total of 16 measurements per station (8 for ground visibility and 8 for 2 m visibility at distances of 5 m and 10 m). The number of visible squares on the checkerboard was counted and a percentage calculated. If a square was more than 50% covered by vegetation, it was considered covered. Overall visibility at the two heights was the mean percentage at 5 m and 10 m. Visibility was determined for ground and 2 m patches but not for 5 m patches because it was not possible to position anyone at this height.

Exposed skyline was used to determine canopy cover. Again a starting point was established directly underneath the patches and measurements were then taken at compass directions NE, NW, SE and SW, at a distance of 1 m from the station. A 50 cm x 50 cm wooden frame was held at a height of 1 m and a photograph was taken from the ground; resulting in a total of 4 measurements per station. The photographs were then imported into ImageJ, a program that calculates the percentage of sky visible through measurement of the number of light pixels. Overall canopy cover was the mean percentage of the 4 measurements.

Data Analysis

All analyses were conducted using IBM SPSS Statistics 19. Significance level was $P = 0.05$. For all experiments, GUD (the number of food items remaining) was square-root transformed to meet assumptions of normality. To measure the effect of increased height from the ground, data were analysed using ANOVA, with GUD as the dependent variable and station and height as independent variables. Station was considered a random effect and accounted for spatial variation. I used linear regressions to test whether there was a relationship between habitat characteristics and GUDs with GUD as the dependent variable and canopy cover and visibility as independent variables.

RESULTS

Summary of results

The array was set up for a total of 60 days and was visited on 24 days. A successful visit was defined as being any occurrence of the monkeys foraging from any food patch as given by GUDs (Table 3.1). Visibility (Table 3.2) and canopy cover are also shown for each station (Table 3.3).

Table 3.1. Total GUD values for all three heights at each station.

Station	Height (m)	Total GUD
1	1	12
1	2	16
1	3	10
2	1	3
2	2	18
2	3	9
3	1	20
3	2	16
3	3	0
4	1	39
4	2	10
4	3	7
5	1	10
5	2	25
5	3	11
6	1	8
6	2	2
6	3	4
7	1	0
7	2	0
7	3	9
8	1	70
8	2	30
8	3	18
9	1	0
9	2	0
9	3	9
10	1	0
10	2	12
10	3	0
11	1	12
11	2	13
11	3	5
12	1	24
12	2	50
12	3	8

Table 3.2. Visibility of each station at heights 0.1 m and 2 m. Values were calculated as the mean percentage at 5 and 10 m.

Station	Height (m)	Visibility (%)
1	0.1	21.84
1	2	54.56
2	0.1	50.95
2	2	53.39
3	0.1	31.95
3	2	32.01
4	0.1	6.11
4	2	25.83
5	0.1	10.61
5	2	29.61
6	0.1	17.11
6	2	9.83
7	0.1	32.11
7	2	47.67
8	0.1	12.78
8	2	52.45
9	0.1	8.17
9	2	56.0
10	0.1	0.0
10	2	47.45
11	0.1	14.95
11	2	37.67
12	0.1	33.12
12	2	48.17

Table 3.3. Canopy cover at each station. Values were measured by calculating the mean percentage of light at 4 compass directions.

Station	Canopy Cover (% light)
1	17.08
2	19.13
3	22.75
4	17.95
5	21.63
6	31.8
7	26.58
8	20.45
9	29.0
10	23.6
11	13.05
12	17.4

GUDs and station height

To test for the effect of height on foraging, I used square-root transformed GUDs at all three heights as the dependent variable, height as a fixed factor and station as a random factor in an ANOVA. The GUDs were the daily values at each height, at each station. Station and height both significantly affected daily GUDs (Station: $F_{11,\ 802} = 5.82$, $P = 0.000$, Height: $F_{2,\ 802} = 7.71$, $P = 0.003$; Figure 3.4). A Tukey HSD multiple comparisons test revealed that GUDs do decline with increasing height and that samangos have significantly lower GUDs in the highest (5 m) patches compared with the middle (2 m) (P

= 0.001) and ground-level (0.1 m) patches (P = 0.007). The 2 m and ground patches did not significantly differ from each other (P = 0.884).

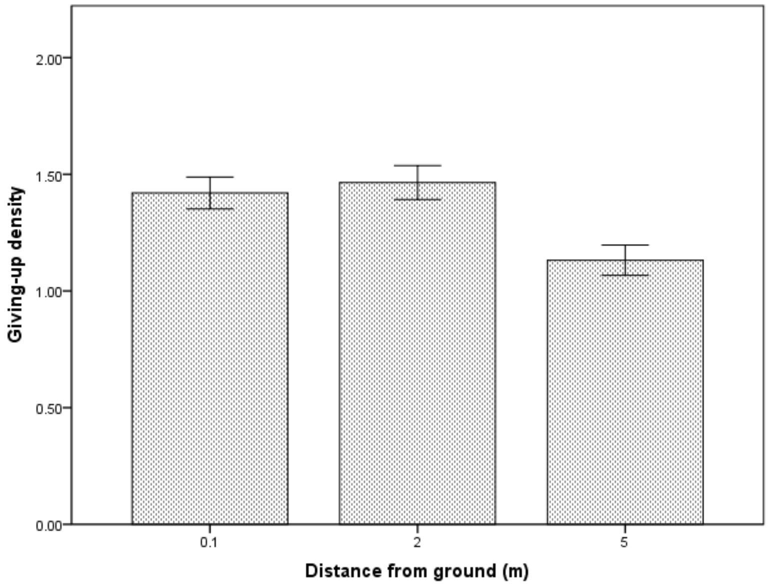

Figure 3.4. Mean giving-up densities at artificial food patches 0.1 m, 2 m and 5 m from the ground. Error bars represent +/- SE.

GUDs and vegetation characteristics

Regression analyses were performed on mean GUDs (square-root transformed) at each of the three heights for canopy cover and at two heights (0.1 m and 2 m) for visibility. The mean GUDs were for each station. Canopy cover significantly affected GUDs ($F_{1, 34}$ = 6.01, P = 0.019; R^2 = 0.15; Figure 3.5) whereas visibility had no significant effect ($F_{1,22}$ = 0.729, P = 0.402, R^2 = 0.032; Figure 3.6). As canopy cover decreases and the percentage of exposed sky increases, GUDs decrease. These results suggest that for this population of samango monkeys, canopy cover is more significant than habitat visibility when making foraging decisions.

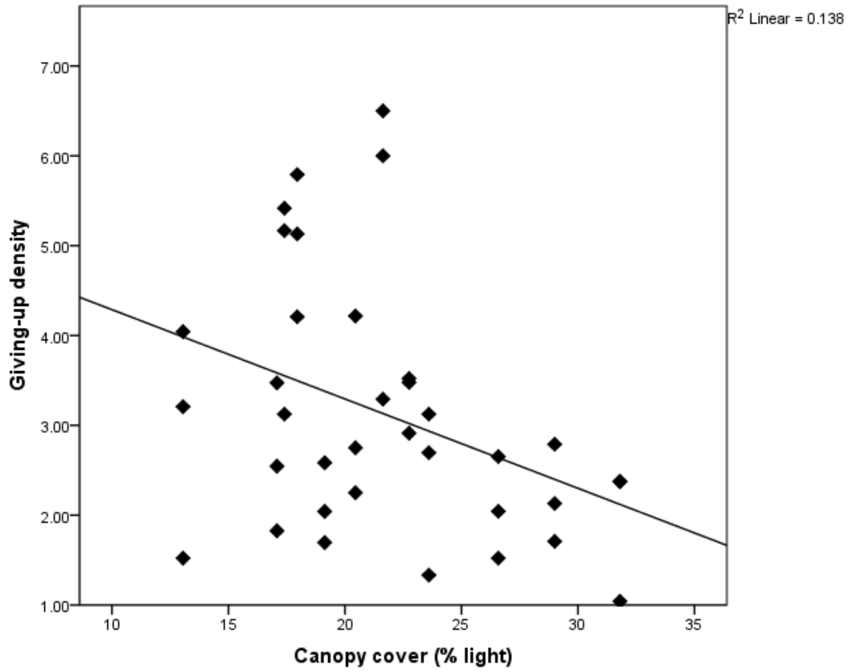

Figure 3.5. Relationship between canopy cover and mean giving-up densities at artificial food patches.

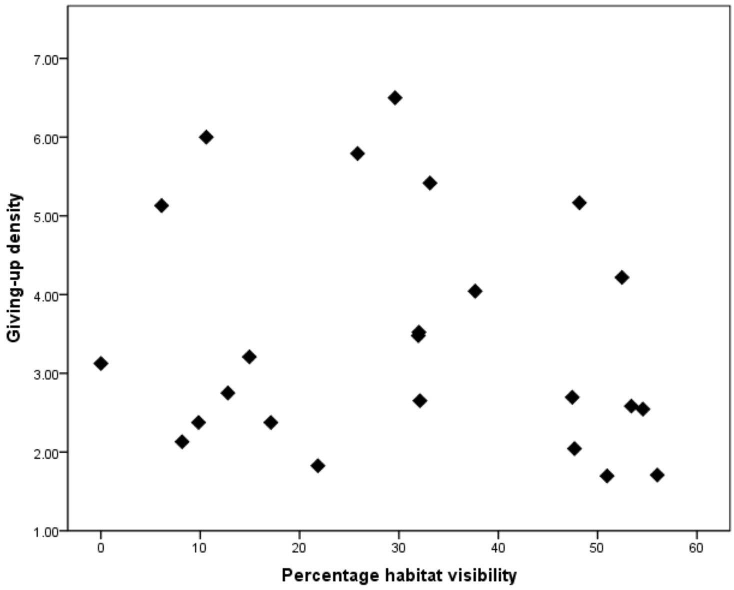

Figure 3.6. Relationship between habitat visibility and mean giving-up densities at artificial food patches.

Out of a total of 12 stations, the highest mean GUD values were found at the three stations (4, 5 and 12) adjacent to the cliffs and all were within 15 m from the cliff wall (Table 3.4; Figure 3.7). Furthermore, the two highest values were recorded at stations 4 and 5, the stations closest to and within sight of the eagle nest (Table 3.4; Figure 3.7; Figure 3.8). A significant relationship was found between distance to nest and mean GUDs (r_s = -0.650, n = 12, p= 0.022). As distance to eagle nest increases, GUDs also increase. It is highly likely that the nest is visible to any foragers located at these two stations. Stations 3, 8 and 11 had values ranging from 2.93 to 3.30. The remaining stations had values ranging from 1.93 to

2.56. These results suggest that the monkeys perceive patches at stations 4, 5 and 12 to be risky and exhibit higher GUDs and therefore, higher foraging costs compared to safer patches.

Table 3.4. Mean GUD values for each of the 12 stations and distance to eagle nest. The values were averaged across the three heights, for a total of 24 visited days. Values in bold are the three highest.

Station	Distance to nest (m)	GUD
1	60.83	2.56
2	41.23	2.11
3	22.36	3.30
4	**10**	**5.04**
5	**10**	**5.26**
6	22.36	1.93
7	41.23	2.07
8	60.83	3.06
9	67.08	2.17
10	50	2.38
11	36.06	2.93
12	**30**	**4.57**

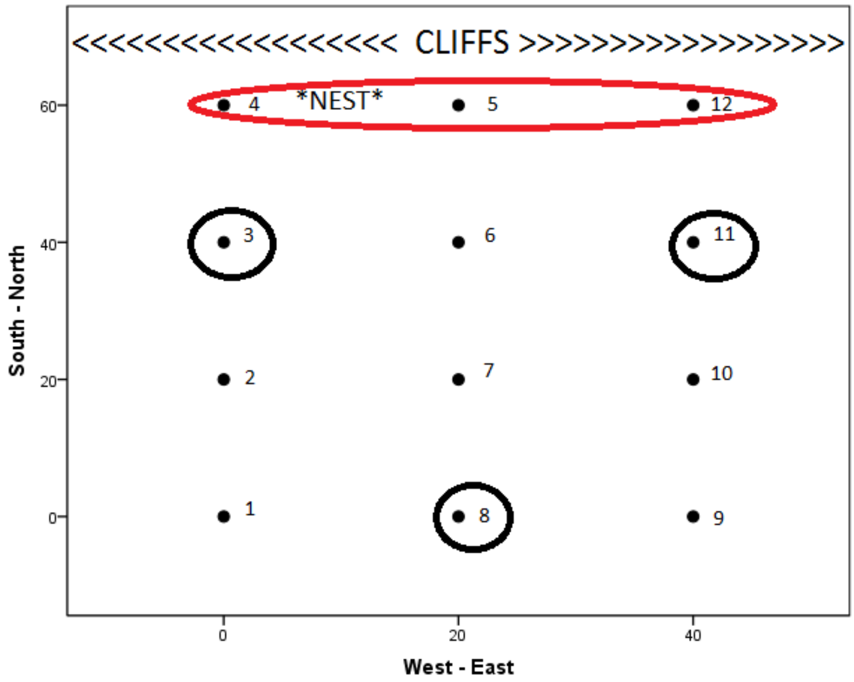

Figure 3.7. The layout of the experimental array with the location of the cliffs and crowned eagle nest. Numbers represent the 12 stations. Red outline (stations 4, 5 and 6) = high GUDs, Black outline (stations 3, 8 and 11) = medium GUDs, No outline (stations 1, 2, 6, 7, 9 and 10) = low GUDs.

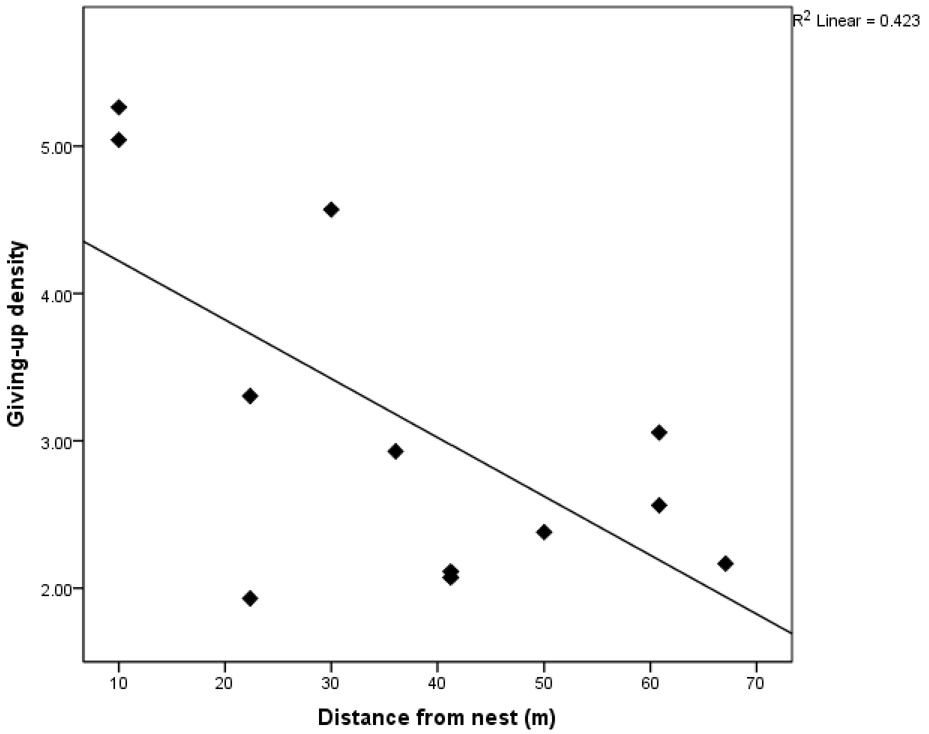

Figure 3.8. The effect of increased distance from crowned eagle nest on mean giving-up densities at artificial food patches.

DISCUSSION

The present study examined the foraging behaviour of samango monkeys using the GUD technique. The main aim was to confirm the height effect found by an earlier study by Emerson et al (2011) and also to determine the effect of canopy cover and habitat visibility on GUDs. The results indicate that samango monkeys treated predation risk as a foraging cost. They appear to perceive a higher predation risk lower to the ground, with GUDs decreasing with increasing height. GUDs were also significantly affected by canopy cover, with GUDs decreasing with decreasing cover. Habitat visibility had no significant effect on GUDs at lower levels in the canopy. The highest GUD values were recorded at stations closest to the crowned eagle nest and cliff wall.

The monkeys exhibited significantly lower GUDs at the top patches (5 m) compared with the middle (2 m) and ground patches (0.1 m). This result confirms the height effect found by Emerson et al (2011) and has also been found in vervet monkeys (Makin et al, 2012); and thick-tailed bushbabies (McArthur et al, 2012) with both species revealing higher GUDs closer to the ground and lower GUDs at patches with increasing height. These results suggest that samango monkeys prefer to forage off the ground. Increased tree height is generally associated with increased predation risk in primates (Struhsaker and Leakey, 1990; de Luna et al, 2010). Crowned and black eagles are significant predators of primates (Mitani et al, 2001; Shultz, 2001) and exposure at the top of the canopy increases the risk of aerial attack. Primates can make up 88 % of a crowned hawk-eagle’s diet in East Africa (Mitani et al, 2001). The results of Emerson et al (2011) could be due to the fact that they did not have a risky patch at the top of the canopy. This location can lead to exposure and increase predation risk from an aerial predator (Chapman and Chapman, 1996; Shultz and Noe, 2002). Their highest food patch was located just below the canopy, hung at a height of 5 m in trees that averaged approximately 6 m in height. This 1 m area above the top patch could have acted as a ‘buffer zone’ and provided a refuge area with sufficient canopy cover that protected the monkeys from any potential aerial attack (Emerson et al, 2011).

The monkeys perceived the same level of risk at a height of 2 m as they did on the ground. The findings of the present study could be more closely related to the results found by Makin et al (2012). Although their study placed patches from the top of the canopy down to the base of the tree, they also found similar GUDs at both the ground level and at 2 m. They suggested that the buffer zone within trees for vervets is from just below the canopy to the base of the tree. This allows safety from both terrestrial and aerial predators. Despite the fact that the present study did not place patches up high in the canopy (this was not possible due to the height of the trees), the buffer zone described by Makin et al (2012) could apply in the case of the present study. The height effect is also demonstrated by vigilance studies. Treves (2002) found that red colobus and redtailed monkeys had higher vigilance when foraging on the ground. This result has been found in a number of primate species including brown capuchins (Hirsch, 2002).

Use of refuges and habitat choice appear to be influenced by predation risk (Rose and Fedigan, 1995). Vegetation is important when considering the foraging behaviour of arboreal primates (Boinski et al, 2003; Enstam and Isbell, 2002; Enstam and Isbell, 2004). An unexpected result was the effect of canopy cover. As canopy cover decreased, GUDs also decreased. This suggests that the monkeys perceive less risk at patches with less vegetative cover. response to increased predation risk, primates should reduce their foraging in open, exposed areas (Shultz, 2001). This makes them increasingly vulnerable to attack from aerial predators. The significant results for canopy cover suggest that samango monkeys foraging behaviour is dependent on the structure of the canopy. Exposed, open canopy can leave an arboreal forager in plain sight of raptors, and vulnerable to attack, especially when the eagles have a sit-and-wait strategy. Foliage across the canopy allows the monkeys to move through the habitat undetected. Cords (1990) found that blue monkeys reduced their vigilance when foliage density increased, thus showing that the monkeys feel safer when there is increased cover. Nonetheless, too much foliage can have negative effects (Boinksi et al, 2003). Increased vegetation cover can work in favour of the primate in that it provides cover and protection but too much cover can also mean that predators can be undetected. This could perhaps explain the canopy effect on GUDs. Higher GUDs were found at patches with higher canopy cover. These patches were considered risky and limited a forager’s ability to accurately monitor its surroundings. This would apply particularly when considering the hunting strategy of eagles. Too much foliage can result in eagles going unnoticed as they perch waiting to ambush unsuspecting prey.

A number of studies have shown that visibility is important in primates when managing predation costs. Visibility had no significant effect on GUDs. This is the opposite to Emerson et al (2011). They found that when sightlines were blocked, GUDs increased. However, they only ran their experiments for 4 days and it could have been that the monkeys were still getting used to the curtains, rather than the obstructed visibility. Coleman (2013) also found that the samango monkeys preferred areas with high visibility. Obstructive cover increases vigilance levels (Treves, 2002). Diana monkeys, *Cercopithecus diana* show an increase in clear calls when habitat visibility is low due to dense vegetation or dark (Uster and Zuberbuhler, 2001). Clear calls in this species are employed primarily to avoid predation. Enstam and Isbell (2004) found that patas monkeys prefer to utilise a tall microhabitat over a short microhabitat. Individuals were frequently observed high up in the trees scanning. Their use of tall trees enhanced their ability to detect predators. Primates are not restricted the ground and can use the increased visibility found higher in the canopy by increasing their height above the ground (van Schaik et al, 1983)..

The highest GUD values were found in the three stations 4, 5 and 12 located adjacent to cliffs that ran from west to east in the study habitat. The monkeys seem to perceive higher predation risk in this area as revealed by their GUDs. The tall trees beside these cliffs are nearly the same height as the cliffs and on two separate occasions, raptors were observed from these patches soaring just above the canopy (R. Sassoon, pers. obs.). These aerial predators have also been observed sitting on the cliff edge and calling and the one occurrence of alarm calls was directed at an aerial predator soaring very close to the top of the canopy. Despite the fact that the highest patch was nowhere near the top of the canopy, the monkeys high GUDs show that they traded foraging effort for safety. Raptors that prey on arboreal primates appear to use stealth and surprise to catch their prey (Mitani et al, 2001; Boinski et al, 2003) or a sit-and-wait strategy where they wait for primates to expose themselves into more open areas in the canopy before they attack (Shultz, 2001). Also, the location of the crowned eagle nest is interesting. Out of stations 4, 5 and 12, the two stations with the highest GUDs, 4 with GUDs of 5.04 and 5, with GUDs of 5.26, were located on either side of it. They were the closest stations located at a distance of approximately 10 m. . Foragers at both these stations would have seen the nest but not at station 12. Despite the fact that no eagles were nesting, the monkeys still seemed to perceive these food patches to be risky and responded by revealing higher GUDs. Another possible reason for such elevated values at these two stations was the canopy cover. Vegetation can provide concealment and reduce predation from aerial predators (Isbell, 1994; Boinski et al, 2003). This area had uneven cover and had a large break in the canopy in which there was none at all. The chance of aerial attack would have been significantly higher at these stations as opposed to stations that were 20 and 40 m south of the array where there was sufficient cover to provide protection. Station 6 merits some discussion. This station revealed the lowest mean GUDs (see Table 3.4), suggesting that the monkeys perceived it to be the lowest risk station of all twelve in the array. What is interesting is that it is located relatively close to the eagle nest at 22.36 m. Also, station 6 is located closer than station 12 to the nest and yet, revealed lower GUD values. It also had the least canopy cover, with a value of 31.8 % (percentage light) and poor visibility at both 1 m (17.11 %) and 2 m (9.83 %). The literature suggests that primates would prefer to forage in areas with adequate canopy cover and good visibility. Location to nest, canopy cover and visibility suggest that this station would be expected to be a risky patch with high GUDs. I suggest that the reason for such low GUD values is based on eagle hunting behaviour. Eagles are ambush predators and employ a sit-and-wait strategy to surprise their prey. At this station, there were no tall trees for the eagles to perch upon and wait. The area was a closed environment, surrounded by foliage and lianas. This is not an ideal habitat for eagles to hunt. Also, the closed environment could have provided protection and concealed the monkeys from soaring eagles just above the canopy or those perching at the eagle nest area.

Station also 8 merits discussion. This station was located 60.83 m from the eagle nest, had a relatively high mean GUD value of 3.06, canopy cover at 20.45% (percentage light) and poor visibility at 1 m (12.78%) and good visibility at 2 m (52.45%). I suggest the reason for such high GUDs was visibility. Facing south, the station was on the edge of a forest gap. Here the habitat was open with very little vegetative cover to provide the monkeys with protection when foraging. Surrounding the gap were tall trees, ideal for perching eagles looking for prey. A foraging monkey could be visible to a hunting eagle at this station. The trade-off between food acquisition and safety is most apparent when considering the habitat characteristics of this station. This station is therefore high risk.

The differing results found between the present study and Emerson et al (2011) are likely due to habitat differences. Their patches were set up in an area of upland scrub forest with a mean canopy height of 7 m. The present study was carried out in an area of tall evergreen forest that is found within pockets of this shorter, scrub forest. Trees in the tall forest can reach heights of 20 m (Hahn, 2006). Makin et al (2012) set up patches from the base of the tree to the top of the canopy. This is unlikely to be possible in the present study habitat due to the tall height of certain trees and accessibility of the patches. However, expanding these methods further and setting up food patches up into the canopy to heights of up to 10 m is potentially possible and would provide additional information on the height effect on harvesting rates. Patches could also be placed on the forest floor at increasing distance from trees to measure spatial variation in the GUDs. Another possibility is to expand on the methods by Makin et al (2012) and set up the patches at the forest edge, with more patches up in the trees and patches at increasing distances from the forest out into the more open, scrub forest. The forest would represent the vertical landscape of fear, the safer habitat, whereas the scrub would represent the horizontal landscape of fear, the riskier habitat.

In conclusion, most primate species perceive greater predation risk closer to the ground, in more open habitats and with reduced visibility. This indicates that habitat structure is important when making foraging decisions. Increased height in trees and canopy cover were the significant factors affecting GUDs for this population of samango monkeys. Habitat visibility did not affect GUDs suggesting that the study habitat provided adequate visibility and clear sightlines required for early predator detection while foraging. The use of GUDs allows direct measurements of habitat characteristics to determine the effects of vegetation on predation risk.

Chapter 4

Foraging behaviour in samango monkeys: the use of giving-up densities and vigilance behaviour.

INTRODUCTION

When weighing foraging options, animals often have to make a trade-off between food and safety. Giving-up densities (GUDs) in depletable food patches and the distribution of foragers across risky and safe food patches are two established methods employed for titrating such a trade-off (Brown and Kotler, 2004). The GUD is the amount of food remaining once a forager has finished harvesting a patch (Brown, 1988). GUD experiments have been successfully employed in a number of studies particularly with rodents (Jacob and Brown, 2000; van der Merwe and Brown, 2008; Abu Baker and Brown, 2010; Kotler et al, 2010) but also with birds (Olssen et al, 2002; Oyugi and Brown, 2003), lagomorphs (Morris, 2005; Abu Baker and Brown, 2009) and ungulates (Altendorf et al, 2001; Hochman and Kotler, 2006; Shrader et al, 2008). Houle et al (2006) used natural GUDs to measure coexistence in blue monkeys (*Cercopithecus mitis*) and redtailed monkeys (*Cercopithecus ascanius*). Despite this, the use of GUDs in primate research is still fairly new and studies have emerged only recently in samango monkeys (*Cercopithecus (nictitans) mitis erythrarchus*: Emerson et al, 2011; Emerson and Brown, in press), thick-tailed bushbabies (*Otolemur crassicaudatus*: McArthur et al, 2012) and vervet monkeys (*Chlorocebus aethiops*: Makin et al, 2012).

Time allocation refers to the location of forager, when it is at that location and for how long it remains there (Brown and Kotler, 2004). These decisions affect the harvest rate and the risk or predation. A forager can adjust the risk and the amount or resources encountered through the selection of habitats and microhabitats, the season or time of day and the length of time in which it spends at a patch (Brown and Kotler, 2004). Opportunities are further optimised by foraging for longer in resource-rich patches and at resource-rich times and risks are avoided by moving between risky and safe times and places. Increased foraging rate results in an increase of harvested resources (Kotler and Brown, 1990). Depletable food patches result in forager effort increasing with time spent foraging (Kotler et al, 1994). This in turn, results in lower GUDs. The number of foragers will also relate to the GUD, with the larger the number of visits, the lower the GUD (Brown, 1988).

Measuring GUDs and behaviour provides a comprehensive data set which enables the separate interpretation and accurate analysis of these two measurements and provides a full examination of the behavioural responses underlying GUDs. Many GUD studies employ the use of cameras. However, often this is to confirm that food patches are visited by the target species and not attributed to another species. In fact, there are very few studies measuring both GUDs and behaviour. In Altendorf et al (2001) and McArthur et al (2012), cameras were used to measure vigilance in mule deer and thick-tailed busbabies respectively. Altendorf et al (2011) predicted that mule deer would reveal higher GUDs and vigilance at forest edges than when in an open habitats and forest interior. They found that vigilance supported this but not GUDs. McArthur et al (2012) increased toxin concentration of food placed in feeders in trees but placed toxin-free feeders on the ground. When on the ground, the bushbabies spent proportionally more time in heightened states of vigilance and when both feeders were toxin free. Higher GUDs were also found in the ground feeders. Hochman and Kotler (2006) employed direct observations with GUDs to determine vigilance and apprehension in Nubian ibex. Predation risk in Nubian ibex is affected by distance to cliff edges and slopes. Increase in distance from slope edge, increases predation risk. They found that risky patches revealed high GUDs and higher vigilance levels. Some GUD studies have highlighted the need for a combined approach using direct behavioural observations (Emerson et al, 2011).

Following the methods of Emerson et al (2011), I applied the GUD technique (Brown, 1988) using artificial food patches to a population of free-living samango monkeys in the western Soutpansberg mountains of South Africa. I then directly observed the monkeys continuously as they began to forage from the patches to when they ceased foraging. Samango monkeys are predominantly arboreal and with aerial predators being the main threat to this population (Coleman, 2013), I made the assumption that increased distance from the ground up into the trees and vegetative characteristics will play key roles in their foraging behaviour. I defined safe patches as ones with (1) increasing height, (2) adequate canopy cover and (3) clear visibility

The aim of this study is to determine the extent to which behavioural measures validate experimental GUD results. No previous study has measured both GUDs and behaviour using direct behavioural observations and attempted to observe foraging behaviour at feeding stations. The following predictions were made:

1. The monkeys would choose to forage from higher patches before foraging from lower patches
2. Total foraging time and total number of foragers would reflect GUDs
3. Lower GUDs with
    a. increasing height
    b. increasing canopy cover
    c. clear habitat visibility
4. Lower vigilance with
    a. increasing height
    b. increasing canopy cover
    c. clear habitat visibility
5. Males will have higher vigilance and lower GUDs than females

METHODS

Study Area and System

The research was conducted at the Lajuma Research Centre in the Soutpansberg Mountains, Limpopo Province, South Africa (29^{o}26E, 23^{o}01 S). The flora of the Soutpansberg is highly diverse (Hahn, 2006) and Lajuma itself is characterised by a diversity of habitats including tall evergreen forest, semi-deciduous woodland, thicket, riverine forest and grassland. The distribution of samango monkeys in South Africa lies primarily within Indian Ocean coastal belt forest and Afromontane forest (Lawes 1990). Habitat fragmentation has resulted in small, geographically isolated populations of these monkeys and the Soutpansberg contains one such population. At Lajuma, the samango monkeys' home range encompasses the evergreen forests, the semi-deciduous woodlands and the riverine forest, as well as the disturbed secondary short forest (Heikamp, 2008). Their diet is primarily frugivorous, along with leaves, flowers and buds but they are opportunistic and will eat insects when encountered (Heikamp, 2008). Samango monkeys are at risk from leopards (*Panthera pardus*), crowned eagles (*Stephanoaetus coronatus*) and black eagles (*Aquila verreauxii*) which all reside at Lajuma.

The GUD Technique

Experimentally, GUDs have been measured by making a depletable food patch in which food is mixed thoroughly into a non-edible substrate in a tray or a tub, using the tray or the tub as the artificial resource patch (Brown, 1988). A small amount of food is used and a large amount of substrate to create the diminishing returns. As the forager harvests the patch, each piece of food must be harder to find than the last. The food must be rich enough to attract and keep the forager at the patch. Yet, the amount of food must be small enough that the animal does not become satiated. The balance between amount of food items and volume of substrate must be correct as the diminishing returns are to cause the forager to leave the patch before all the food items have been harvested (Emerson et al, 2011). The substrate increases search time and encourages diminishing returns. The artificial food patch gives the GUD for the most efficient forager. Often this is the last forager to have harvested thoroughly from the patch. If less efficient foragers visit later, they will not gain any rewards from exploiting the patch. However, if a more efficient forager visits the patch later, it will gain reward from harvesting the patch. The GUD as the animal leaves the patch is a measure of its foraging costs. Therefore, the patch is insensitive to the number of foragers that visit.

Depletable food patches, yielding giving-up densities were used to measure the foraging costs of predation in samango monkeys. Methods employed to measure GUDs follow Emerson et al (2011). Artificial food patches were generated by thoroughly mixing 25 raw, dry peanut halves with 4 litres of untreated eucalyptus sawdust in plastic tubs (15 cm high, 45 cm diameter). To test the vertical landscape of fear in samango monkeys, food patches were hung at different heights in 12 trees, approximately 20 m apart, in a 3 x 4 grid in an area of tall evergreen forest. Patches were baited at 0930 hours and sieved at 1600 hours, where the remaining peanut halves were counted. Patches were prepared in late morning to allow for the troop to move off from the sleeping site. Often, patches were visited by several monkeys. Peanuts were never found on the ground but on occasions, sawdust was spilled from the tubs. If spilled sawdust was 1 litre or more, the datum from that food patch was excluded from the analysis. Whenever extensive spillage occurred, the sawdust was restocked back to 4 litres the following day ready for data collection. Regardless of extensive spillage, every few days the tubs were restocked with sawdust to maintain the correct volume that was potentially reduced through continual foraging, wind and sieving. The experiments were run from 11th of April until 15th of July and resulted in 19 successful visits.

Patches were sieved every day, even if the monkeys had not visited. Only days with visits were included in the analysis. On such days, it was very rare for patches to be left untouched. This happened on only one occasion during the study. The foraging station, rather than individual foragers was the unit of replication in this study. GUDs are insensitive the number of foragers and typically correspond to the last forager that visited (Hochman and Kotler, 2006). Lajuma has two habituated troops of samango monkeys that have adjacent home ranges. The location of the experimental array was in a core area of one of the troops' home range and covered an area of 2400 m^2. The habitat was an area of tall evergreen forest with tree heights of up to 20 m. This contrasts with Emerson et al (2011). Their study habitat was an area of upland scrub forest with a mean canopy height of 7 m.

Foraging Behaviour

Behavioural observations were employed using continuous sampling (Altmann, 1974). Data collection started as soon as the first individual began to forage at a patch. The tree (station) was the focal point, rather than the individual monkey to ensure that observations started with the first forager to visit that food patch. Observers, usually two at a time, were positioned apart and between 3 and 5 metres from the tree to minimise observer effect. Data collection started as soon as a monkey made contact with a tub. Often the monkeys positioned themselves on the trunk of the tree and pulled the tubs toward them to gain better position ready to search. Once the monkey had the tub in the right position and had sufficient hold of it, it would begin to search (Figure 3.1). A foraging bout started as soon as an individual physically touched the tub and ended when the forager physically let go of the tub. If a monkey was still holding the tub or inside it, but not searching, this was still counted as a foraging bout as it could possibly want to continue foraging. The height (0.1m, 2m or 5m), age/sex class of the forager (adult male, adult female or subadult), vigilance and the start and finish of the foraging bout was noted to calculate duration at each height (Table 4.1). Large body size, comparatively long canines and presence of scrotum were used to identify males. Presence of prominent nipples distinguished females from subadults. Also, females are generally larger than subadults. Sex differentiation was not possible in subadults due to absence of nipples.

Vigilance was characterised into four component behaviours and the total of these components (Table 4.2). Such component behaviours may serve different functions: predation or social (Hirsch, 2002; Treves, 2000). Look-ups were defined as a forager raising its head in order to focus its attention in one direction, with no left to right movement of head. Scans were defined as side to side head movements. Social vigilance was defined as the number of glances directed at a conspecific but only when the conspecific is in view and can be identified as the source of the vigilance. Observer vigilance was defined as the number of glances directed at field observers. The total was the sum of all four components.

Table 4.1 Description of information collected during behavioural observations.

Data	Definition
Station	Station 1-12
Time Start	Time the monkey began foraging in a tub
Time Finish	Time the monkey finished foraging in a tub
Height	Foraging in 0.1 m, 2 m or 5 m tub
Age/Sex Class	Male, Female, Subadult
Vigilance	4 component behaviours (see Table 4.2)

Table 4.2 . Definition of vigilance components.

Vigilance	Definition
Look-ups	Raising of head to focus visual attention in one direction, no side to side movement of head
Scans	Raising of head, followed by side to side movements enabling the monkey to look left and right
Conspecific	Raising of head and looking directly at group mates. Must see second forager
Observer	Raising of head and looking directly at field observers
Total	Total of all of the above categories

Figure 4.1. Samango monkey foraging from a food patch.

Vegetation Characteristics: Exposed Skyline and Habitat Visibility

To determine the relationship between vegetation and vigilance, visibility and canopy cover were measured at each of the 12 stations. For visibility, the starting point was directly underneath the patches. Measurements were then taken at the four cardinal compass directions (N, S, E and W) at distances of 5 m and 10 m away. A 75 cm x 75 cm board marked out as a 5 cm checkerboard was placed at heights of 0 m and 2 m at both distances. A photograph was taken at the same height as the checkerboard, resulting in a total of 16 measurements per station (8 for ground visibility and 8 for 2 m visibility at distances of 5 m and 10 m). The number of visible squares on the checkerboard was counted and a percentage calculated. If a square was more than 50% covered by vegetation, it was considered covered. Overall visibility at the two heights was the mean percentage at 5 m and 10 m.

To measure exposed skyline, again a starting point was established and this was directly underneath the patches. Measurements were then taken at compass directions NE, NW, SE and SW, at a distance of 1 m from the station. A 50 cm x 50 cm wooden frame was held at a height of 1 m and a photograph was taken from the ground; resulting in a total of 4 measurements per station. The photographs were then imported into ImageJ, to calculate the proportion of ‘light’ and ‘dark’ pixels. Overall canopy cover was the mean percentage of the four dark pixel measurements.

Data Analysis

All analysis was conducted using IBM SPSS Statistics 19. Significance level was P = 0.05. For all experiments, GUD (the number of food items remaining), vigilance (mean rate of look-ups, scans, conspecific, observer and total were square-root transformed to meet assumptions of normality.

RESULTS

Summary of Results

The study yielded a total of 19 days for behavioural data. Subadults make up a large proportion of the foragers with 61 visits. Females visited 24 times and males visited 4 times (Table 4.3). A monkey will enter the array, select a food patch and often forage in all patches at that station (tree), sometimes monopolising the station (R. Sassoon, personal observation). The monkey then moves on to another station and repeats this behaviour. This repeated behaviour frequently resulted in every food patch being visited and also, being visited several times, most likely by different foragers. Therefore, the majority of the troop was observed foraging from the food patches. The monkeys would enter the array in 3 or 4 small foraging groups and time between groups could be up to an hour. This allows the foragers to spread out in the forest and monopolise stations. The larger the foraging group, the less monopolising of stations and more displacements as competition for patches increased. The majority of foragers were subadults, with females and the dominant male. During the mating season, 3 males were observed in the array; the dominant male and two immigrant males.

Table 4.3 . Summary of results showing the total number of visits, the total duration and vigilance occurrences, and the rates for each age/sex class.

Age/Sex Class	Total Visits	Total Duration (minutes)	Average Duration (per minute)	Total Vigilance	Rate of Vigilance (per minute)
Male	4	5.27	1.32	4	0.76
Female	24	68.53	2.86	181	2.64
Subadult	61	119.48	3.27	455	2.28

Height preference and foraging order

The monkeys were observed at the stations 19 times and behavioural data collected on these days (N = 19). To examine the height preference of the monkeys, an ANOVA was used with height order as the dependent variable and height as the independent variable on the first foragers to visit a patch. There was a significant effect of height with the monkeys showing a preference for the top patch at 5 m ($F_{2, 47}$ = 5.45, P = 0.007; Figure 4.2). A Tukey HSD multiple comparisons test revealed that there were significant differences between the top and ground patch (P = 0.006) but not the middle patch (P = 0.686). There was no difference between the ground and middle patches, although the relationship approached significance (P = 0.083).

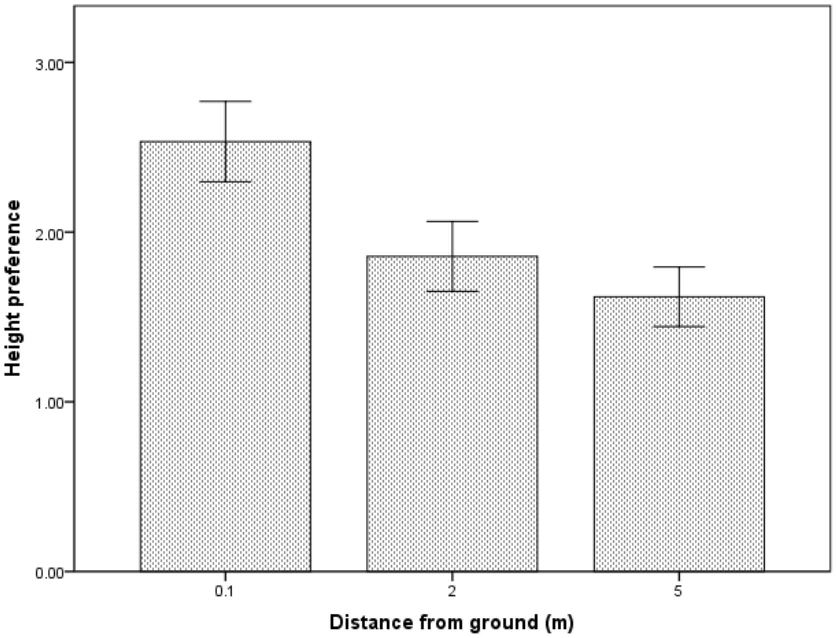

Figure 4.2. Height preference at artificial food patches at 0.1 m, 2 m and 5 m from the ground. Error bars represent +/- SE.

GUDs and forager effort

To test the hypotheses that total foraging time and total number of foragers reflect GUDs, I used linear regressions with GUD as the dependent variable and time and foragers as the independent variables. Separate regressions show significance for both time ($F_{1,\,52}$ = 19.53, P = 0.000; R^2 = 0.273) and foragers ($F_{1,\,52}$ = 8.45, P = 0.005; R^2 = 0.140). As both foraging time and forager number increases, GUDs decrease (Figures 4.3 and 4.4). When the relationships were combined in a single regression, a significant relationship was found between time and GUDs ($F_{2,\,51}$ = 9.58, P = 0.004; R^2 = 0.273) but not foragers ($F_{2,\,51}$ = 9.58, P = 0.946; R^2 = 0.273).

The monkeys foraged from the array 19 times (N = 19). To test for the effect of height on GUDs at all three heights, I used GUD as the dependent variable, height as a fixed factor and station as a random factor in an ANOVA. Station and height significantly affected daily GUDs (Station: $F_{11,\,633}$ = 6.05, P = 0.000, Height: $F_{2,\,633}$ = 9.52, P = 0.001; Figure 4.5). A Tukey HSD multiple comparisons test revealed that GUDs do decline with increasing height and that samangos have significantly lower GUDs in the highest (5 m) patches compared with the 2 m (P = 0.002) and ground-level patches (P = 0.003). GUDs in the middle (2 m) and ground patches (0.1 m) did not significantly differ from each other (P = 0.987).

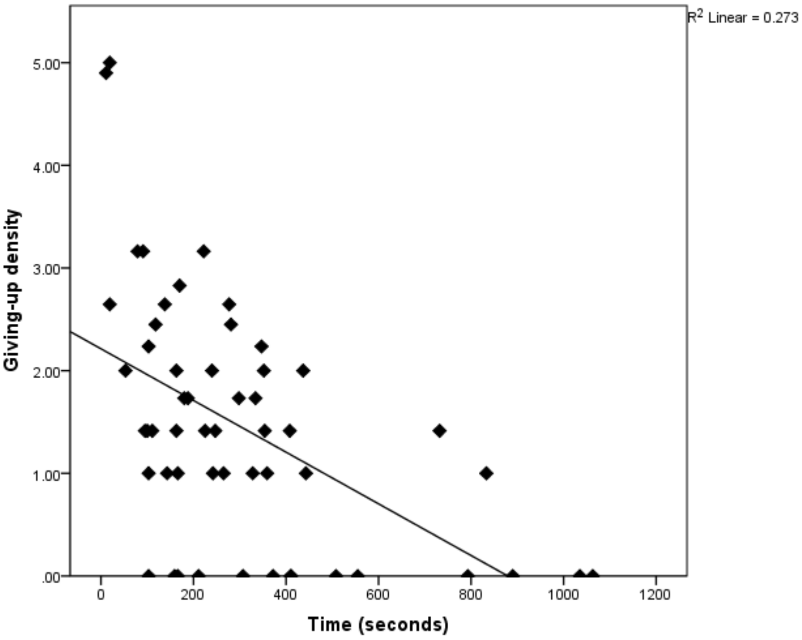

Figure 4.3. Relationship between time and mean giving-up densities at artificial food patches**.**

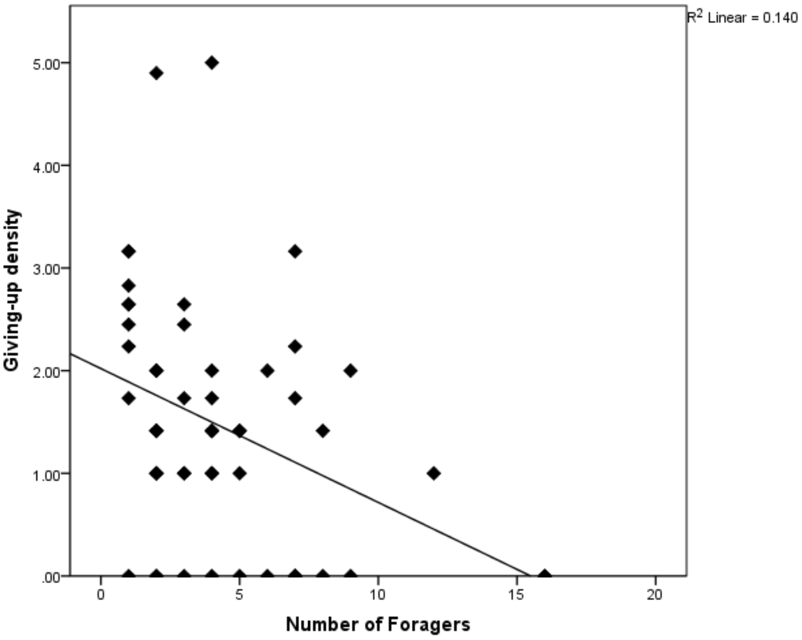

Figure 4.4. Relationship between total number of foragers and mean giving-up densities at artificial food patches.

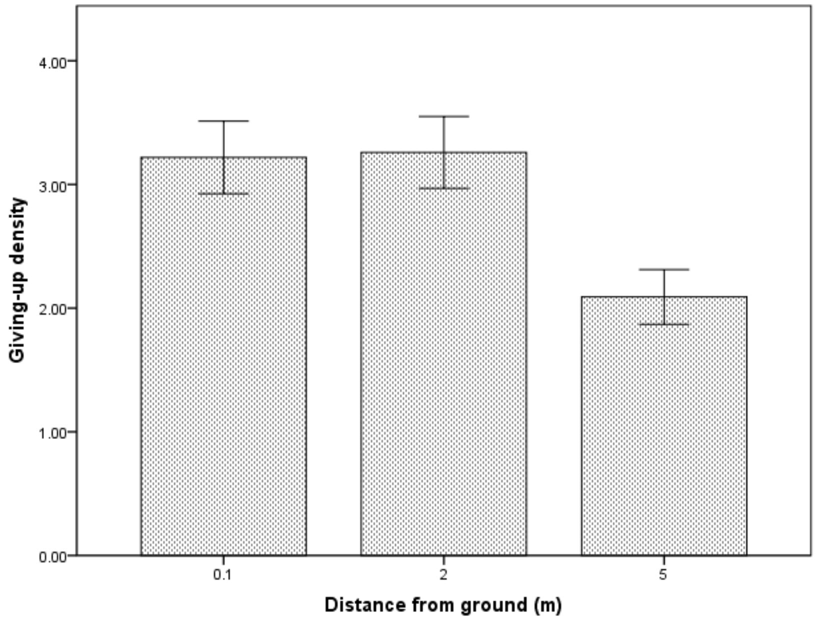

Figure 4.5 Mean giving-up densities at artificial food patches 0.1 m, 2 m and 5 m from the ground. Error bars represent +/- SE.

Vigilance and station height

To test for the effects of height on vigilance level, I used the four component behaviours of vigilance and total vigilance (look-ups, scans, observer and conspecific) as dependent variables and height as the independent variable in an ANOVA. Only conspecific vigilance was significant with height (Table 4.4 ; Figures 4.6-4.10), with ground and top patches differing from each other (P = 0.034) but no such difference between the ground and middle patches (P = 0.289) or between the middle and top patches (P = 0.547). There was significantly more vigilance directed at conspecifics at 5 m, compared with 0.1m and 2m (Figure 4.6).

Table 4.4 . Results of ANOVA showing the effects of height on the mean rate of vigilance.

Vigilance	$F_{(2, 51)}$	P
Look-ups	1.929	0.156
Scans	0.184	0.833
Observer	0.849	0.434
Conspecific	3.355	0.043
Total Vigilance	0.244	0.784

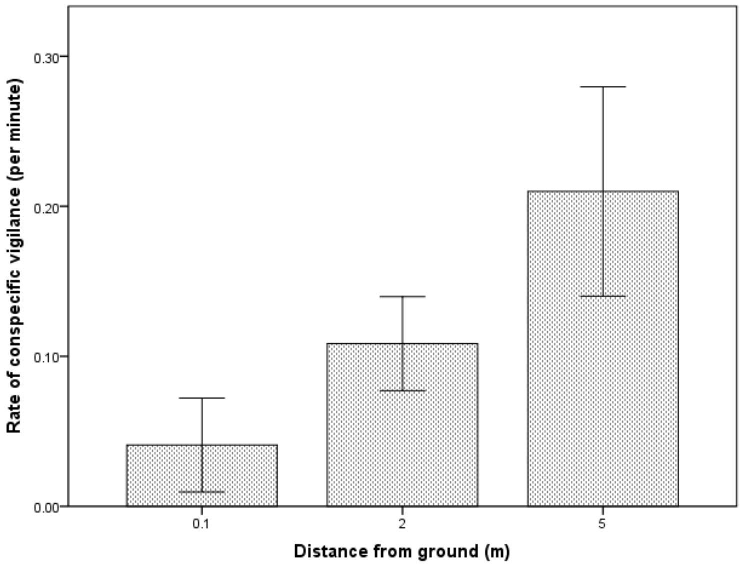

Figure 4.6. Mean rate of vigilance directed at conspecifics at artificial food patches 0.1 m, 2 m and 5 m from the ground. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

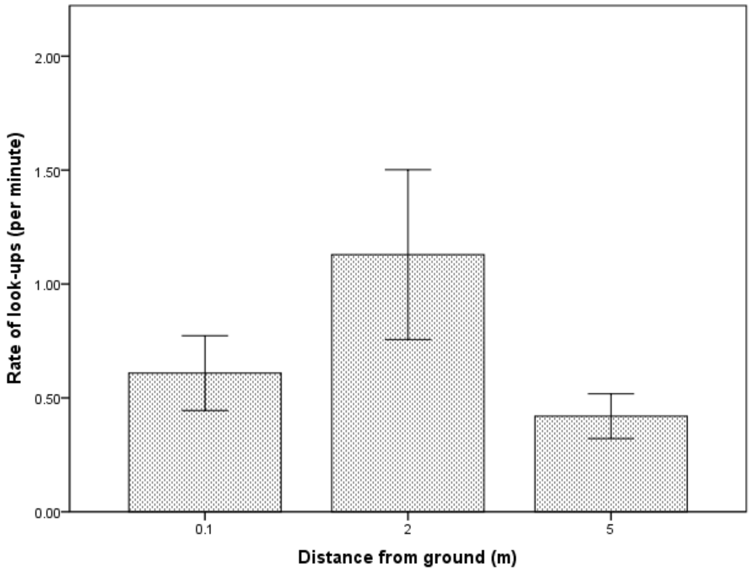

Figure 4.7. Mean rate of look-ups at artificial food patches 0.1 m, 2 m and 5 m from the ground. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

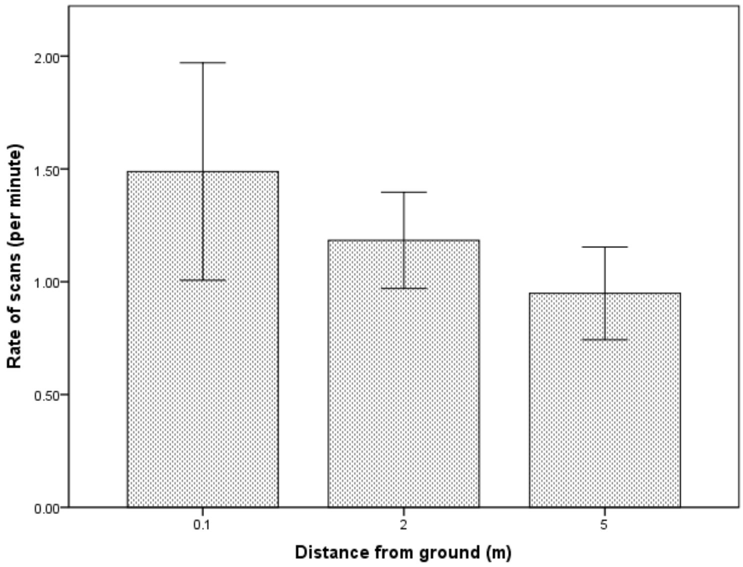

Figure 4.8. Mean rate of scans at artificial food patches 0.1 m, 2 m and 5 m from the ground. Vigilance is expressed as occurrences per minute. Error bars represent +/- SE.

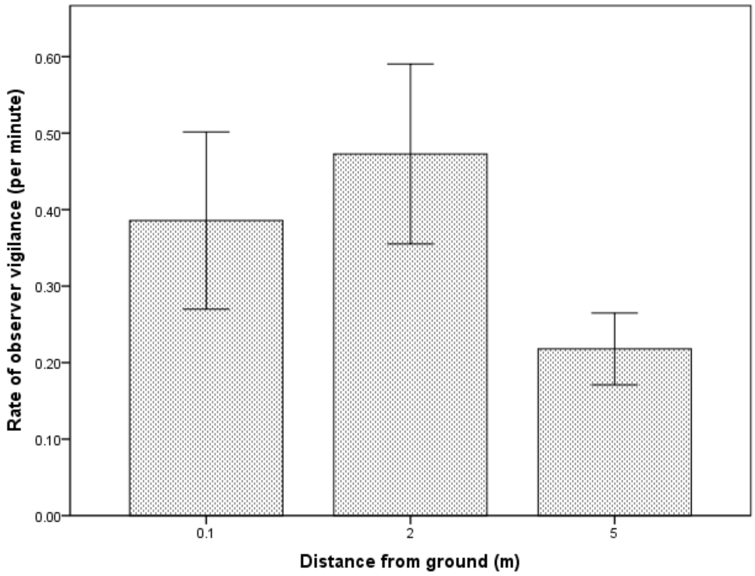

Figure 4.9. Mean rate of vigilance directed at field observers at artificial food patches. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

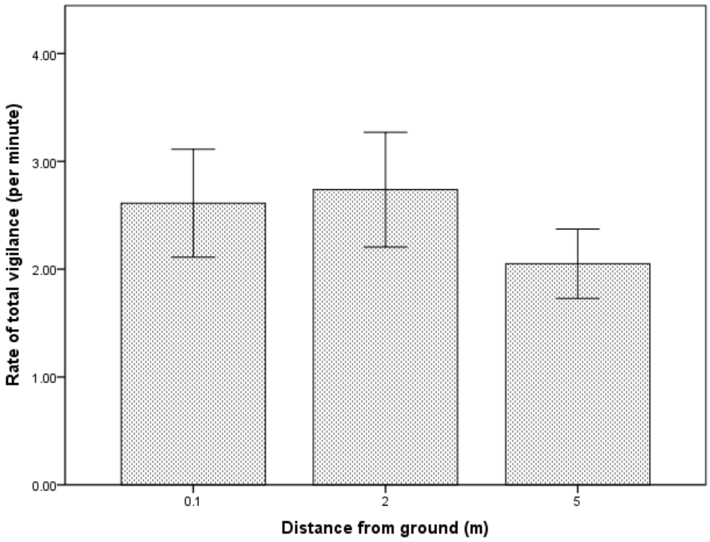

Figure 4.10. Mean rate of total vigilance at artificial food patches 0.1 m, 2 m and 5 m from the ground. Vigilance is expressed as total occurrences (look-ups, scans, conspecific and observer) per minute. Error bars represent +/- SE.

Vigilance and vegetation characteristics

I performed linear regressions to determine the effect of canopy cover (exposed sky) and habitat visibility on vigilance rates for the four component behaviours and total vigilance. There were significant effects of canopy cover on observer vigilance ($F_{1,\ 34}$ = 4.461, P = 0.042; R^2 = 0.116; Figure 4.11) and conspecific vigilance ($F_{1,\ 34}$ = 5.487, P = 0.025; R^2 = 0.139; Figure 4.12). As the percentage light increases and canopy cover decreases, both observer and conspecific vigilance increase. There was no effect of canopy cover on look-ups ($F_{1,\ 34}$ = 0.331, P = 0.569; R^2 = 0.010; Figure 4.13), scans ($F_{1,\ 34}$ = 0.331, P = 0.810; R^2 = 0.059; Figure 4.14) or total vigilance ($F_{1,\ 34}$ = 0.009, P = 0.924; R^2 = 0.000; Figure 4.15).

There was no significant effect of habitat visibility on any of the component vigilance behaviours. Look-ups ($F_{1,\ 22}$ = 0.177, P = 0.678; R^2 = 0.008; Figure 4.16), scans ($F_{1,\ 22}$ = 2.00, P = 0.171; R^2 = 0.083; Figure 4.17), observer ($F_{1,\ 22}$ = 0.250, P = 0.622; R^2 = 0.011; Figure 4.18), conspecific ($F_{1,\ 22}$ = 1.31, P = 0.265; R^2 = 0.056; Figure 4.19) and total ($F_{1,\ 22}$ = 0.812, P = 0.377; R^2 = 0.036; Figure 4.220).

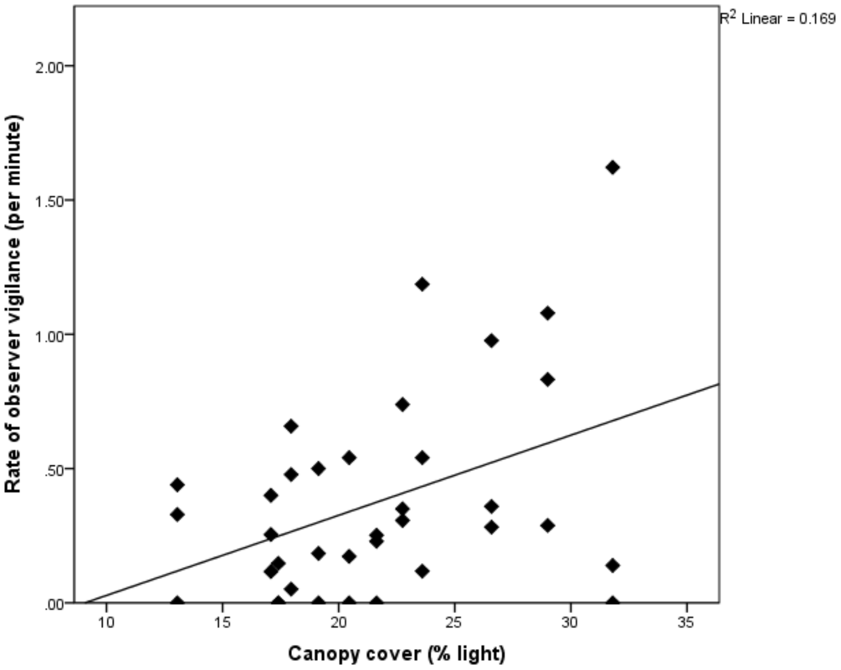

Figure 4.11. Relationship between canopy cover and mean rate of vigilance directed at field observers at artificial food patches. Vigilance is expressed as glances per minute.

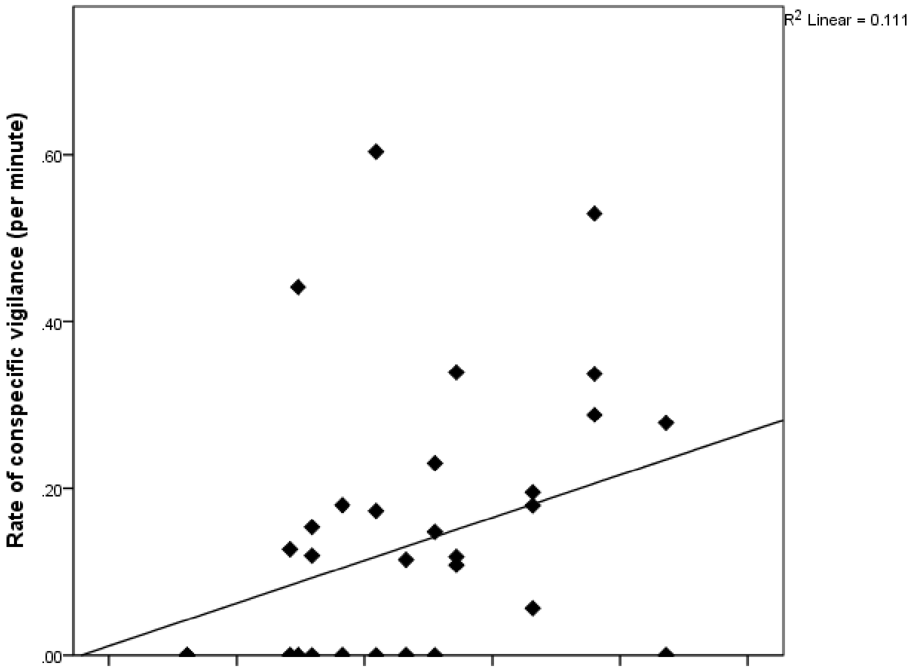

Figure 4.12. Relationship between canopy cover and mean rate of vigilance directed at conspecifics at artificial food patches. Vigilance is expressed as glances per minute.

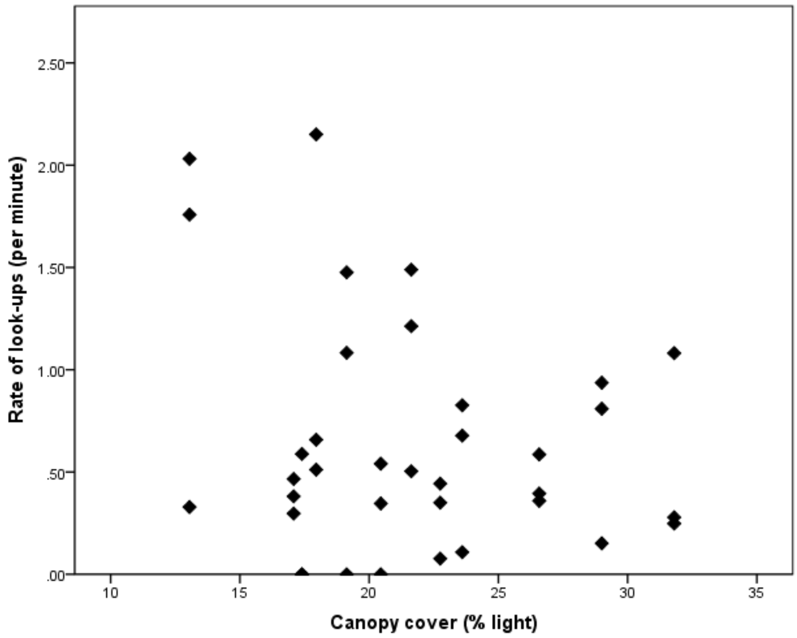

Figure 4.13. Relationship between canopy cover and mean rate of look-ups at artificial food patches. Vigilance is expressed as glances per minute.

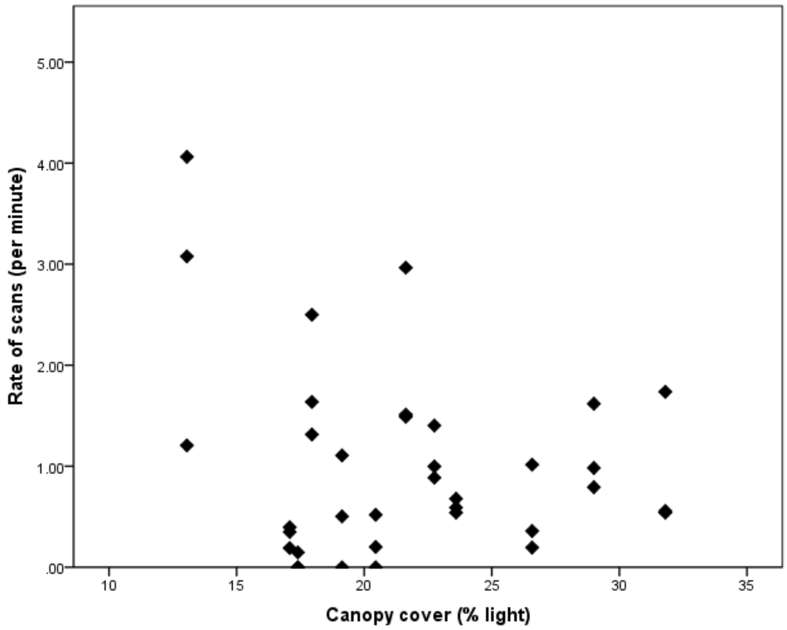

Figure 4.14. Relationship between canopy cover and mean rate of scans at artificial food patches. Vigilance is expressed as occurrences per minute.

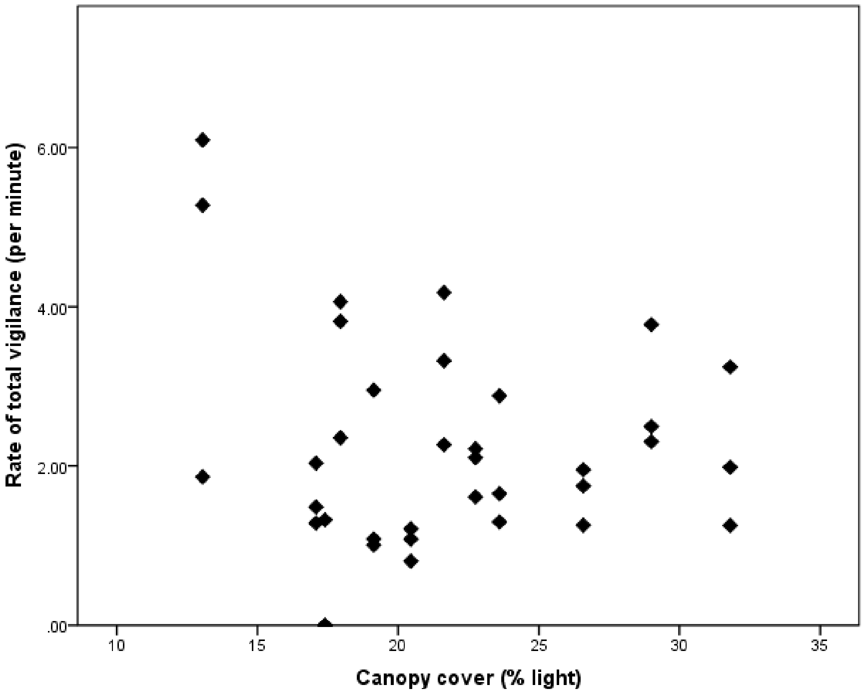

Figure 4.15. Relationship between canopy cover and mean rate of total vigilance at artificial food patches. Vigilance is expressed as total occurrences (look-ups, scans, conspecific and observer) per minute.

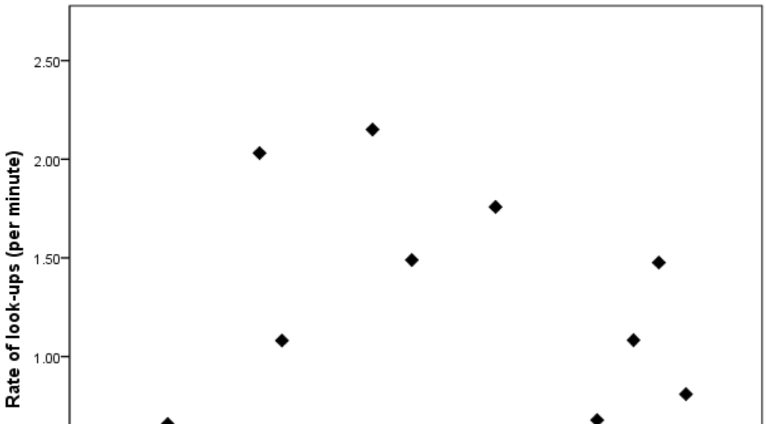

Figure 4.16. Relationship between habitat visibility and mean rate of look-ups at artificial food patches. Vigilance is expressed as glances per minute.

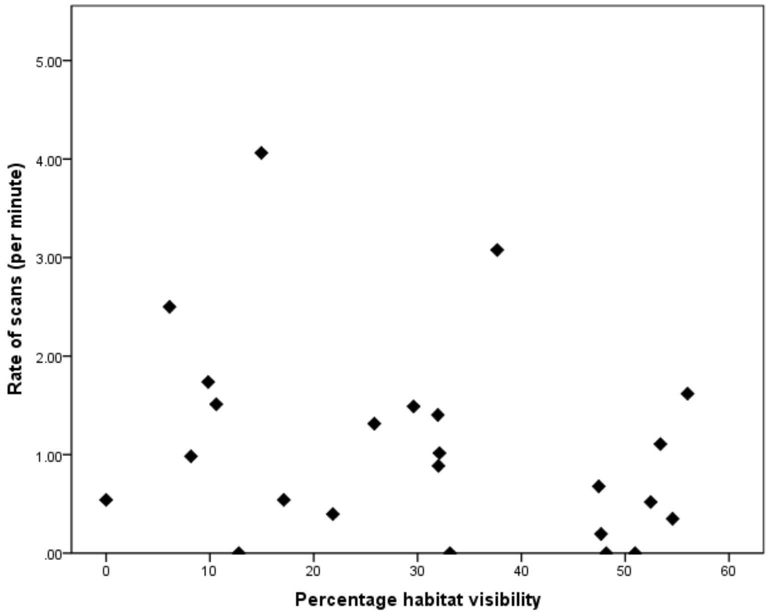

Figure 4.17. Relationship between habitat visibility and mean rate of scans at artificial food patches. Vigilance is expressed as occurrences per minute.

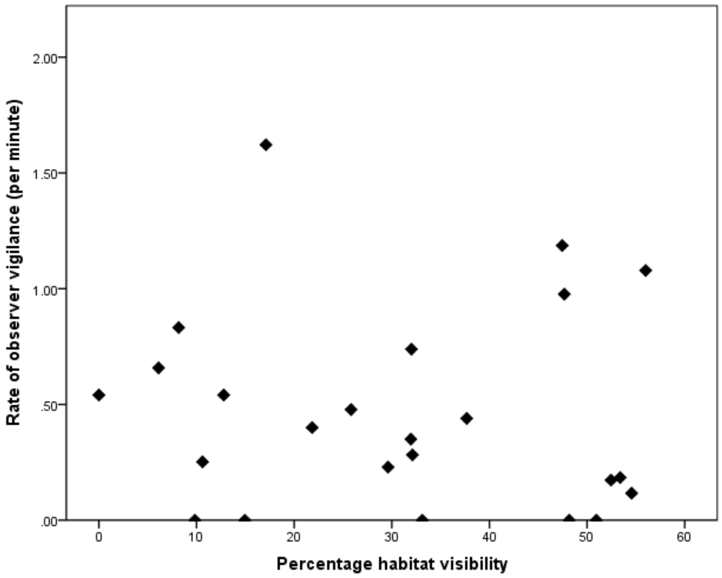

Figure 4.18. Relationship between habitat visibility and mean rate of vigilance directed at field observers at artificial food patches. Vigilance is expressed as glances per minute.

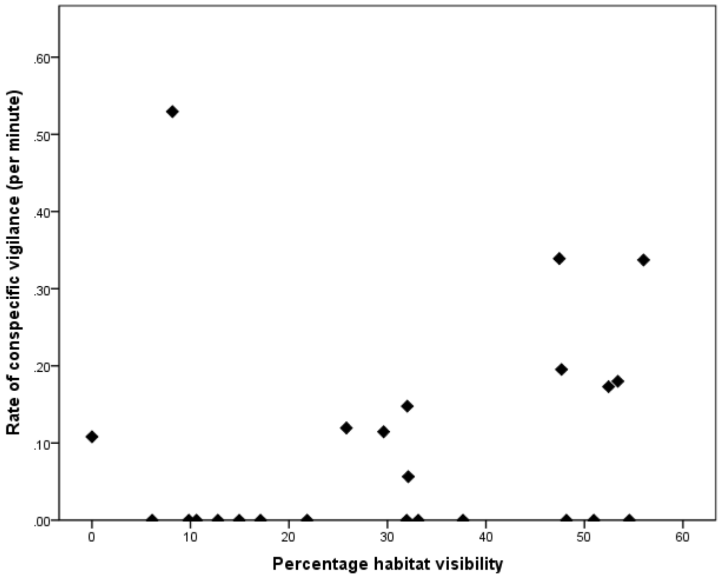

Figure 4.19. Relationship between habitat visibility and mean rate of vigilance directed at conspecifics at artificial food patches. Vigilance is expressed as glances per minute.

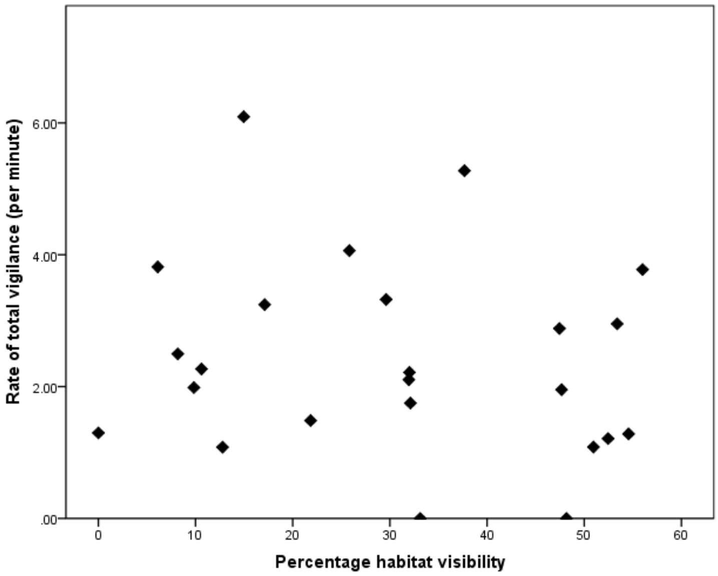

Figure 4.20. Relationship between habitat visibility and mean rate of total vigilance at artificial food patches. Vigilance is expressed as total occurrences (look-ups, scans, conspecific and observer) per minute.

Vigilance and Age/Sex Class

Age/sex differences in vigilance were examined using ANOVAs with the four component behaviours of vigilance, plus total vigilance as dependent variables and forager as the independent variable. Age/Sex had significant effects on look-ups, observer and total vigilance, with subadults being more vigilant than males and females (Table 4.5; Figures 4.21-4.25). No significance was found for scans or conspecific vigilance (Table 4.5; Figures 4.24 and 4.25). A Tukey HSD multiple comparisons test revealed that for look-ups, subadults differed significantly from males ($P = 0.008$) but not females ($P = 0.209$) and no difference between males and females ($P = 0.115$). For observer vigilance, subadults differed significantly from males (P = 0.007) and females (P = 0.031) but no difference between males and females (P = 0.267). For total vigilance, subadults differed significantly from males (P = 0.003) and females (P = 0.038) but no difference between males and females (P = 0.142).

Table 4.5 . ANOVA showing the effects of age/sex class on the square-root of vigilance.

Vigilance	$F_{(2, 87)}$	P
Look-ups	5.274	0.007
Scans	2.25	0.111
Observer	6.681	0.002
Conspecific	0.075	0.927
Total Vigilance	7.415	0.001

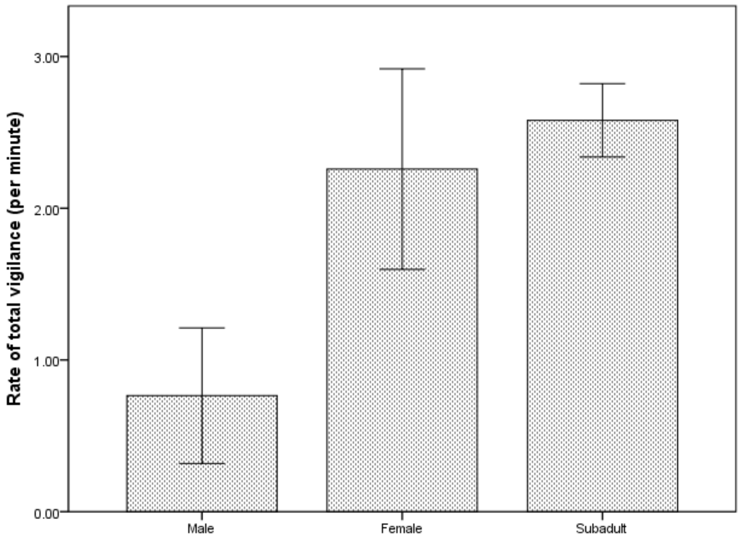

Figure 4.21. The effect of age/sex class on the mean rate of total vigilance at artificial food patches. Vigilance is expressed as total occurrences (look-ups, scans, conspecific and observer) per minute. Error bars represent +/- SE.

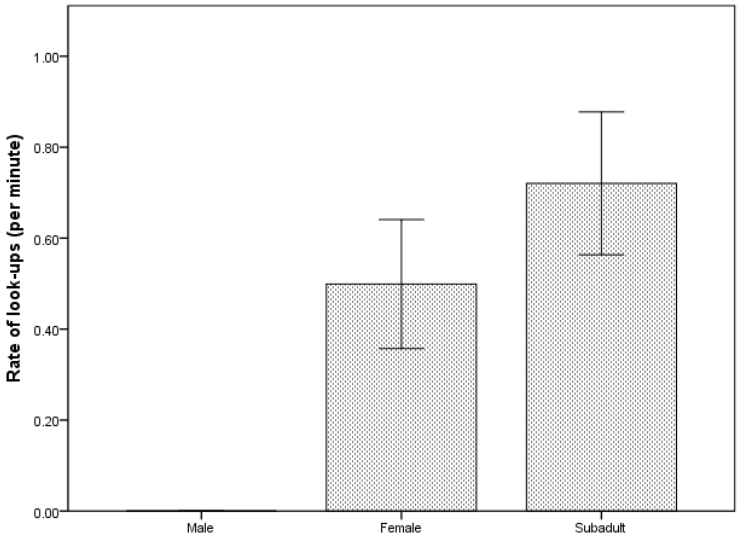

Figure 4.22. The effect of age/sex class on the mean rate of look-ups at artificial food patches. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

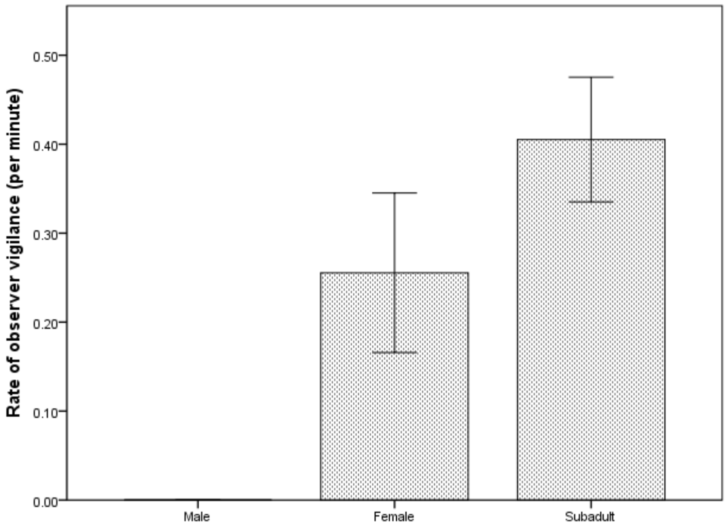

Figure 4.23. The effect of age/sex class on the mean rate of vigilance directed at field observers at artificial food patches. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

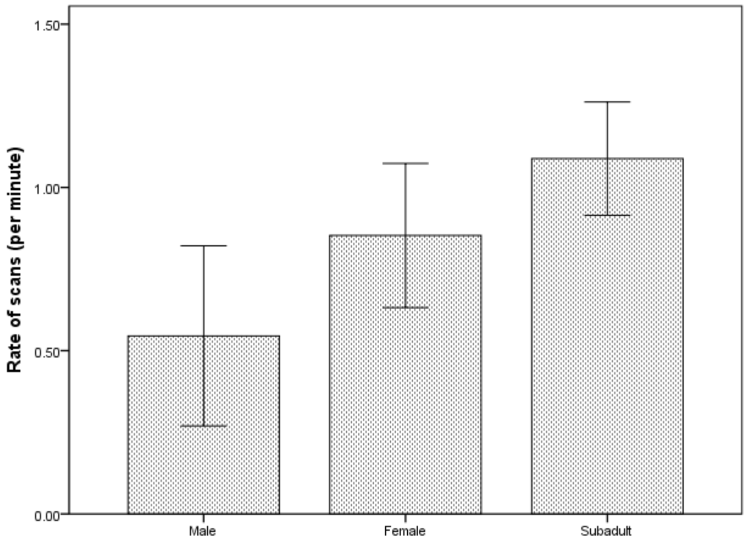

Figure 4.24. The effect of age/sex class on the mean rate of scans at artificial food patches. Vigilance is expressed as occurrences per minute. Error bars represent +/- SE.

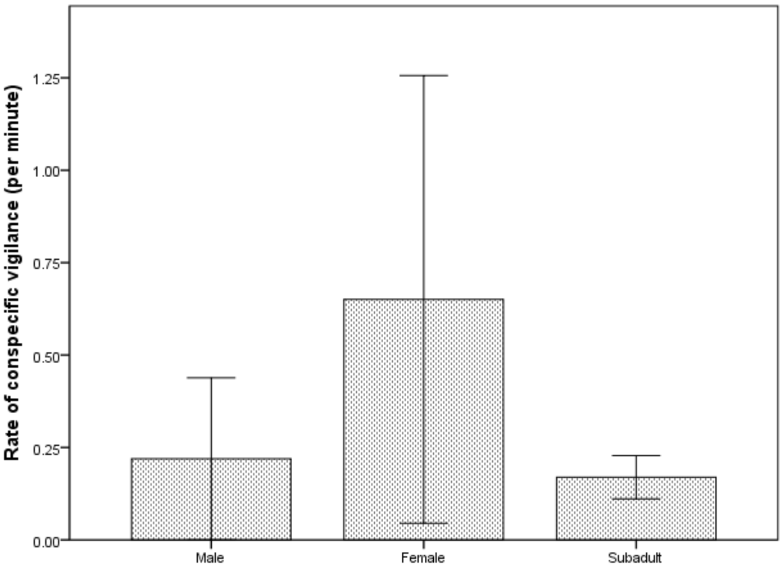

Figure 4.25. The effect of age/sex class on the mean rate of vigilance directed at conspecifics at artificial food patches. Vigilance is expressed as glances per minute. Error bars represent +/- SE.

DISCUSSION

The monkeys showed a preference for the 5m patch and often visited that height first. Frequently individuals would monopolise a station at the top patch, then move down and begin searching in the 2m patch and finally, in the ground patch. Forager effort also matched GUDs, with an increase in foragers resulting in a decrease in GUDs.

Despite GUDs and vigilance not being entirely consistent, there were some interesting results. The monkeys revealed decreasing GUDs with increasing height, with the lowest GUDs at the top patches. Conspecific vigilance was significantly affected by height, conspecific and observer vigilance were affected by canopy cover and visibility had no significant effect on vigilance.

The monkeys revealed lower GUDs as height increased, with significantly lower GUDs at the top patches (5 m) compared with the two lower patches, suggesting that their predation costs decrease with increase in height. This height effect on GUDs is supported by other primate studies, including Emerson et al (2011). Vervet monkeys (Makin et al, 2012) and thick-tailed bushbabies (McArthur et al, 2012) revealed lower GUDs as distance from the ground increased. These results suggest that these primates perceive higher predation risk closer to the ground and that they treat height as an important factor when making foraging decisions. Despite this, height is associated with increased predation risk in primates (Struhsaker and Leakey, 1990; Isbell, 1994; de Luna et al, 2010). The top of the canopy provides little or no vegetative cover and increases the risk of detection and therefore, predation from an aerial predator (Isbell, 1994; Chapman and Chapman, 1996; Shultz and Noe, 2002).

There was a significant effect of height on conspecific vigilance but not any other measurement of vigilance. As height increased, conspecific vigilance increased. Vigilance behaviour in primates has two roles; social and predation risk but the relationship between height and vigilance serves as an anti-predatory response to increased predation risk and not as a social monitoring response (Hirsch, 2002). A number of primate studies have found that vigilance decreases with increased height in tree. McArthur et al (2012) found that at ground feeders, thick-tailed bushbabies spent proportionally more time in heightened states of vigilance (alert and alarmed) compared to tree feeders. Treves (2002) found that red colobus, *Procolobus badius* and redtailed monkeys have higher vigilance when foraging on the ground. This result has been found in other primate species including brown capuchins, *Cebus apella* (Hirsch, 2002), blue monkeys, *Cercopithecus mitis* (Gaynor and Cords, 2012), chimpanzees, *Pan troglodytes schweinfurthii* (Kutsukake, 2006), Thomas's langurs, *Presbytis thomasi* (Steenbeek et al, 1999), ursine colobus monkeys, *Colobus vellerosus* (MacIntosh and Sicotte, 2009; Teichroeb and Sicotte, 2012), woolly monkeys, *Lagothrix lagotricha poeppigii* (Di Fiore, 2002), saddleback (Saguinus fuscicollis) and moustached tamarins (Saguinus mystax (Smith et al, 2004). The main predators of this population are eagles (Coleman, 2013) but perhaps the threat of such predation could nonetheless be rather minimal, resulting in low levels of vigilance (Hirsch, 2002).

There was a significant effect of canopy cover on conspecific and observer vigilance but not any other measurement of vigilance. As canopy cover decreased, both measurements of vigilance increased. Habitat is an important factor when considering the behaviour of arboreal primates (Boinski et al, 2003; Enstam and Isbell, 2002; Enstam and Isbell, 2004). Use of refuges and habitat choice appear to be influenced by predation risk (Cords, 1990, Rose and Fedigan, 1995; Cowlishaw, 1998). In response to increased predation risk, primates should reduce their foraging in open, exposed areas (Shultz, 2001) and move to an area with high foliage density or an understory tree trunk (Isbell, 1994). Raptors use stealth and surprise to catch their prey or a sit-and-wait strategy where they wait for primates to expose themselves into more open areas in the canopy before they attack (Mitani et al, 2001; Shultz, 2001; Boinski et al, 2003). Exposed canopy can leave the monkeys in plain sight of raptors, and vulnerable to attack. On the other hand, vegetative cover across the canopy provides protection. Cords (1990) found that blue monkeys reduced their vigilance when foliage density increased, suggesting that the monkeys feel safer when there is increased cover. Cheek pouches can be employed to reduce predation risk (Lambert, 2005). If foraging in a risky area, samango monkeys can fill their cheek pouches before moving to a safer area, one with increased foliage density. Nonetheless, too much foliage can have negative effects (Boinksi et al, 2003). Increased vegetation cover can provide cover but can also obscure vision and result in predators being undetected. I suggest that the lack of significant effect of canopy cover on foraging behaviour is due to the fact that the study habitat provides the monkeys with sufficient, mostly continuous vegetative cover required to reduce detection from raptors. The monkeys can allocate more time to foraging and less time to vigilance.

There was no significant effect of visibility on vigilance. A number of studies have shown that visibility is important in primates when managing predation costs. Obstructive cover increases vigilance levels (Treves, 2002). Diana monkeys, *Cercopithecus diana* show an increase in clear calls when habitat visibility is low due to dark or dense vegetation (Uster and Zuberbuhler, 2001). Clear calls in this species are employed primarily to avoid predation. Enstam and Isbell (2004) found that patas monkeys prefer to utilise a tall microhabitat over a short microhabitat. Individuals were frequently observed high up in the trees scanning. Their use of tall trees enhanced their ability to detect predators. This is related to height in trees. Primates are not restricted the ground and can use the increased visibility found higher in the canopy by increasing their height above the ground (van

Schaik et al, 1983). One might assume that primates would be more vigilant when in open habitats on the ground. Jaffe and Isbell (2009) found that vervets were less vigilant in open areas. Their suggestion was that the monkeys did not need to increase their vigilance levels due to the clear visibility. The main predator of vervets in their study was leopards. As leopards hunt by ambushing or stalking their prey, they rely on dense vegetation for a successful kill (Chase Grey, 2011). Emerson et al (2011) found that GUDs in samango monkeys were significantly affected by blocked sightlines but not by ground vegetation. Emerson et al (2011) used curtains to block sightlines and the experiment was run for six days. It could have been the novelty of the curtains that caused a significant effect rather than the blocked sightlines. The present study found no significant effect of visibility on vigilance levels. This suggests that either the monkeys do not require clear sightlines when foraging or that the vegetation of the study habitat was sparse enough to allow the monkeys an adequate view of their surroundings.. I propose that primates do use sightlines when foraging and that it is the habitat characteristics that are the cause for the lack of significant results.

The present study is the first to demonstrate the use of GUDs and direct behavioural observations to measure predation risk. Other studies incorporating behaviour with GUDs have used cameras rather than direct observations. These studies do not provide a comprehensive measurement of vigilance. This study’s direct behavioural measurements enable a more detailed interpretation of the actual foraging behaviour at the feeding stations. Observers were present before the monkeys entered the array and began foraging from the stations and were there when the monkeys finished foraging and left the array. This is the first study that has collected behaviour as the target species is actually foraging from the feeding stations. Three known studies that have measured GUDs and behaviour merit some discussion. These studies measured GUDs and vigilance in mule deer (Altendorf et al, 2001), Nubian ibex (Hochman and Kotler, 2006) and thick-tailed bushbabies (McArthur et al, 2012). Altendorf et al (2001) set up cameras 2 m from risky feeding trays. As the animal approached a tray, its picture was taken. Consecutive shots were then taken every two minutes and the pictures categorised as either vigilant (head up) or foraging (head down). Hochman and Kotler (2006) carried out behavioural observations within 2.30 h after sunrise and 2.30 h before sunset, the period when Nubain ibex are most active. Each focal sample bout lasted 3 minutes. Behaviour was classified into vigilance, feeding and other behaviours. McArthur et al (2012) used motion-sensitive infrared video cameras to record behaviour at one of the 4 study sites. Cameras were set on high sensitivity level for 20 s duration and measured when visits occurred and for how long the bushbaby visited the feeder. Each study provided a measure of vigilance, although the data were limited when compared to direct observations. In the mule deer study, data were lost as the camera only took pictures every two minutes or when the camera was triggered by a new forager. In the Nubian ibex study, vigilance data were collected during two time periods, just before sunset and sunrise. Again, data were lost as there are no continual observations. On the other hand, this study did use direct observations to monitor vigilance. The thick-tailed bushbaby study only recorded foraging behaviour for 20 seconds. To observe a forager from the start of a feeding station visit until the end is the only accurate method to measure behaviour and allow comparisons to be made with GUDs. Behavioural measurements validate the GUDs in two out of the three studies described above. With the bushbabies, risky patches revealed high GUDs and high vigilance and the same for the Nubian ibex. The mule deer study found that vigilance was highest at risky patches but that this was only found in the GUDs.

Group size can have an effect on foraging behaviour (Janson and Goldsmith, 1995). The study troop has approximately 40 members and when foraging the group spread out far across the canopy to exploit resources. In terms of the experimental array, the monkeys did not visit as a whole group. Foragers often visited in small foraging groups, usually of three or four individuals, with up to two hours between visits. The foraging behaviour of these monkeys appeared dependent on the size of the foraging group, with an increase in foraging group size causing an increase in agonistic behaviour at the food patches, although these data were not analysed here.

Social variables cannot be overlooked as significant factors influencing an individual’s predation risk and foraging decisions (Lima and Dill, 1990). Primates are among the most social of animals with 73% travelling with one or more adult conspecifics (Wrangham 1987) .Many species live in troops with dominance hierarchies (Koenig, 2002). These hierarchies are often linear and maintained through agonistic interactions in the form of aggression and displacements. Higher ranking individuals frequently have access to the best food resources resulting in lower ranking individuals being subject to poorer quality resources. In the case of the present study where metabolic and missed opportunity costs were kept constant, one could make the assumption that the best patches are the ‘safer’ patches that offer safety from predators, rather than those that offer higher energetic returns. Safer patches are defined as top patches in trees, with good canopy cover and clear visibility for early detection of terrestrial and aerial predators (Boinski et al, 2003). The result is dominant individuals monopolising these particular patches. Subordinates can either wait until such patches are free or they can harvest from riskier patches that could potentially increase their predation risk.

A secondary aim of the present study was to expand upon the results found by Emerson et al (2011), coupling behavioural observations with GUDs. Comparable results were the height and the vegetation effects. Despite the differences found at ground and 2 m patches, both studies found a decrease in GUDs with increase in height in Emerson et al (2011) visibility was significant for the monkeys when sightlines were blocked. Both studies used artificial patches consisting of peanut halves mixed with sawdust and set up at heights of 0.1 m, 2 m and 5 m. The slightly different results are likely to be due to habitat differences. The tall forest of the present study has trees more than twice the height of the scrub forest where Emerson et al (2011) set up their experimental array. It also has an almost closed canopy, the key habitat characteristic required for arboreal species. The tall forest is also one of the choice habitats of this population (Coleman 2013) suggesting that as well as providing the monkeys with the food resources that they require, it is likely that it is also a safe area in which to forage, rest or engage in social behaviour such as grooming and play. It is also the location of their main sleeping site, providing the troop with the tall trees and lianas required to protect them from terrestrial predators such as leopards. Timing may also have had an effect. The present study ran from April until July, whereas Emerson et al (2011) ran from July until August and the different months may have had a seasonal effect on the monkeys. During the winter months, the monkeys spend much of their time in Acacia scrub forest, whereas the summer months are mostly spent in the tall forest.

In conclusion, most arboreal primate species perceive greater predation risk closer to the ground, in areas with open, exposed canopy and with reduced visibility. The aims of this study was to validate GUDs with behavioural measures. The monkeys do experience a vertical landscape of fear as revealed by their GUDs but only conspecific vigilance was significantly affected by height. Look-ups, scans and observer vigilance were not influenced by height. The tall forest was a preferred habitat of these monkeys and has particular features that reduce predation risk. Adequate canopy cover provides protection from aerial predators when higher in trees. Good visibility and clear sightlines ensure early detection of both aerial and terrestrial predators. I suggest that the lack of significant results found for the behavioural observations is due to social factors, mainly group size. The many eyes and dilution effect can also reduce predation risk and subsequently lead to a reduction in anti-predatory behaviour.

Chapter 5

Discussion

The present study had two main objectives. First, to replicate and expand upon the methods of Emerson et al (2011). Second, to validate and examine the relationship between GUDs and vigilance behaviour and to determine the extent to which experimental approaches match observed behaviour. To summarise, the monkeys revealed decreasing GUDs with increasing height, decreasing GUDs with decrease in canopy cover but no significant effect of habitat visibility on GUDs. The highest GUD values were found to be at food patches adjacent to the cliffs and nearest to the crowned eagle nest. Conspecific vigilance was significantly affected by height, and conspecific and observer vigilance were significantly affected by canopy cover. Habitat visibility had no significant effects on any of the component vigilance behaviours. Age/sex class had significant effects on GUDs, look-ups, observer vigilance and total vigilance. Males revealed higher GUDs than both females and subadults.

The monkeys revealed lower GUDs as height increased, with significantly lower GUDs at the top patches (5 m) compared with both the middle (2 m) and ground patches (0.1 m). Furthermore, the middle patch and the ground patch showed similar GUD values. These results suggest that the monkeys perceive predation risk to be lower the higher they are in the trees and also that they perceive a similar level of risk at a height of 2 m as they do on the ground. These results differ slightly from that of Emerson et al (2011). Their results showed a significant decrease of GUDs with increasing height. This relationship between foraging and height in trees found by Emerson et al (2011) is surprising due to the fact that the main threat to this population of samango monkeys is eagle predation (Coleman, 2013) and increased height in the canopy is normally related to greater predation risk from aerial predators (Struhsaker, 1967; Struhsaker and Leakey, 1990). Crowned and black eagles are significant predators of arboreal primates (Mitani et al. 2001; Shultz, 2001) and both these predators co-occur with samango monkeys at this site. In East Africa, primates can make up 88% of a crowned hawk-eagle's diet (Mitani et al. 2001). The top of the canopy provides limited vegetative cover to arboreal species and increases the risk of exposure and attack from the air (Isbell, 1994; Chapman and Chapman, 1996; Shultz and Noe, 2002). Emerson et al (2011) suggested that the location of their top patch provided a possible explanation for the positive relationship between foraging and height. Their 5 m patch was hung 1 m below the canopy. This 1 m difference could have acted as a ‘buffer’, a safe zone that provided the monkeys with adequate canopy cover that protected them from any potential aerial attack and allowed the predation costs to be lower at 5 m than at 2 m (Emerson et al. 2011). The present study did not place patches close to the top of the canopy. Nonetheless, canopy cover of the tall forest is >80 % (Coleman, 2013) which was the site the experimental array in this study. The location could thus explain the differing results found between the studies. Nonetheless, both studies reported a significant decrease in GUDs from 2 m to 5 m suggesting that perceived predation risk declines with increasing height from the ground.

The monkeys showed a preference to forage in the top patch before the middle and ground patches with significant differences found between the top and ground patches. The height effect on foraging behaviour has already been discussed and this height preference seems to mirror the relationship found between height and GUDs; that predation risk is increased closer to the ground and the monkeys forage more and lower GUDs, higher up in the trees. The general behaviour of the monkeys was to enter the array at a height of approximately 5-10m. A forager then selected a tree and descended to the 5 m patch to begin searching (Rachel Sassoon, pers. obs.). The preference for the 5m and significance found between the top and ground patches suggests that the monkeys consider the top patches to be safer than the ground patches and choose to forage from patches furthest from the ground first, before deciding whether to descend to lower heights and forage at the middle and ground patches. There was no significant difference between the top and middle patches. This result differs to the results found for GUDs, where it was the top patch that differed from both the middle and ground patches. In terms of height preference, it seems that the monkeys are choosing to forage in 5 m and 2 m patches before the ground patches. A possible reason for this is certain foragers would not have ventured to forage at the ground patches. The monkeys’ preference for the top patch is not surprising given their arboreal nature and the fact that they spend the majority of their time in trees and very little time in lower layers of the forest. Different arboreal primate species show differing height preferences in the forest strata. In the Ituri Forest in the Democratic Republic of Congo, blue monkeys spend much of their time above 10 m (Thomas, 1991) and given the choice of a ‘tall microhabitat’ and a ‘short microhabitat’, patas monkeys will choose the tall habitat (Enstam and Isbell, 2004). Another example is in the lesser spot-nosed monkeys (*Cercopithecus petaurista*) of the Ivory Coast’s Tai Forest. These monkeys are found in the top layer of the understory and are rarely found in the lowest levels of the forest (shrub and ground levels) (McGraw, 2000). Thick-tailed bushbabies revealed higher GUDs at toxin-free artificial patches on the ground compared to toxin-free patches placed in trees (McArthur et al, 2012). These primates are at most threat from terrestrial predators and when startled, the typical response is to retreat to a safe vantage point in trees (Estes, 1992). These species may differ in their vertical use of space in the canopy and understory of their forest habitats but all prefer to forage in trees rather than on the ground.

Of the five components of vigilance behaviour, only conspecific vigilance was significantly affected by height. It was predicted that vigilance would decrease with increasing height. However, the results showed the opposite with conspecific vigilance increasing with increasing height. A possible reason could be due to the arboreal nature of the monkeys and relate to intra-group competition. Although samango monkeys show low intra-group aggression (Cords, 2002a), competition is likely to increase with an increase in number of neighbours. This could be most apparent higher in the canopy. Also, if predation risk decreases with height, foragers can perhaps afford to direct their vigilance towards conspecifics and reduce predator vigilance. There was significantly less conspecific vigilance at the ground and middle patches. A possible reason for this is that vigilance at lower heights could be antipredatory rather than social given the threat of terrestrial predation (Struhsaker, 1967; Isbell, 1994). However, this was not the case in the present study. Height had no significant effect on look-ups, scans, observer and total vigilance suggesting that vigilance levels are not affected by increased height from the ground. The lack of significance is surprising. However, given that the tall forest is one of their preferred habitats (Coleman, 2013). It could be that the monkeys consider this habitat as a safe area in which to forage and therefore, the height effect is cancelled out. The habitat provides adequate canopy cover and contains the tall trees that the samango monkeys prefer. Despite the lack of significance found in four of the component behaviours, there are some interesting results. Most notable being that all four showed lower rates at the 5 m patch compared to the middle and ground patches. This follows the hypotheses that vigilance decreases with increasing height from ground and suggests that potentially the monkeys were being less vigilant higher up. Furthermore, scans were revealed to decrease as height increased, thus showing that potentially there could be a height effect on the scanning behaviour of the monkeys. The middle patch had a higher rate of look-ups. Enstam and Isbell (2004) found that patas monkeys preferred tall vegetation to short vegetation and the taller the tree, the higher they would position themselves in the tree. They suggest that the monkeys may prefer to utilise a tall habitat because the trees provide a better vantage point from which to scan and observe the surroundings. It could be that the samango monkeys are showing similar behaviour. Two metres from the ground may not seem like a great distance, and it is more likely that a height of 5 m may be preferred over a height of 2 m. However, maybe that 2 m covers just enough distance from the ground to allow a forager to be vigilant. Observer vigilance was also highest at the 2 m patch. As already discussed, perhaps height in a tree allows a forager to be more vigilant. On the other hand, an observer could be a potential threat to a foraging samango even though the monkeys are fully habituated. It could be that the 5 m patch provides safety up high but as the monkey moves down to forage at lower patches, its vigilance increases to include glances at observers. Looking at total vigilance, this is most closely related to the GUD results with a decrease from 2 m to 5 m and the ground and 2 m patches revealing similar rates. Only when the second forager could be seen visually, was vigilance considered social. It could often be difficult to determine if vigilance was being directed at conspecifics as the dense foliage frequently obscured foragers, especially if a monkey was stationary. In most cases, an observer is only aware of a monkey if it is moving. If it moves silently, as they do in the understory, it can be missed entirely (Rachel Sassoon, pers. obs). Potentially, there were more instances of social vigilance that could not be identified and caution should be taken when considering the significant relationship between height and conspecific vigilance.

A number of primate studies have documented a decrease in vigilance with increasing height in tree. Vigilance behaviour in primates has two roles; social and predation risk but the relationship between height and vigilance serves as an anti-predatory response to increased predation risk and not as a social monitoring response (Hirsch, 2002). McArthur et al (2012) found that at ground feeders, thick-tailed bushbabies spent proportionally more time in heightened states of vigilance (alert and alarmed) compared to in tree feeders. Treves (2002) found that red colobus, *Procolobus badius* and redtailed monkeys have higher vigilance when foraging near the ground than in trees. This result has been found in other primate species including brown capuchins, *Cebus apella* (Hirsch, 2002), blue monkeys (Gaynor and Cords, 2012), chimpanzees, *Pan troglodytes schweinfurthii* (Kutsukake, 2006), Thomas's langurs, *Presbytis thomasi* (Steenbeek et al, 1999), ursine colobus monkeys, *Colobus vellerosus* (MacIntosh and Sicotte, 2009; Teichroeb and Sicotte, 2012), woolly monkeys, *Lagothrix lagotricha poeppigii* (Di Fiore, 2002) and saddleback, *Saguinus fuscicollis* and moustached tamarins, *Saguinus mystax* (Smith et al. 2004).

It was predicted that vigilance would decrease with increasing canopy cover. Of all five components of vigilance behaviour, two were significantly affected by canopy; observer and conspecific vigilance. Both components increased with decrease in canopy cover. Canopy cover was measured by calculating the percentage light. As the percentage light increased from 13.05 to 31.8, vigilance directed at observers and conspecifics increased.

The decrease in cover by 18.75 % is likely to be significant to the monkeys. They may not have shown an increase in rates of look-ups or scanning behaviour but they did show an increase in social vigilance. A possible reason for this increase is the increased predation risk. The monkeys are aware that there is a decrease in canopy cover and are monitoring conspecifics more in case another forager spots a potential threat. The result for observer vigilance suggests that with a decrease in vegetative cover, the monkeys are more apprehensive. Therefore, observers become a potential threat and require that more vigilance is directed at them. Despite the lack of significance, scans appear to show a decrease as canopy cover decreases.

Vegetative structure is an important factor when considering the behaviour of arboreal primates (Boinski et al. 2003; Enstam and Isbell, 2002; Enstam and Isbell, 2004). Use of refuges and habitat choice appear to be influenced by predation risk (Cords, 1990, Rose and Fedigan, 1995; Cowlishaw, 1998). In response to increased predation risk, primates should reduce their foraging in open, exposed areas (Shultz, 2001) and move to an area with high foliage density or an understory tree trunk (Isbell, 1994). Raptors use stealth and surprise to catch their prey or a sit-and-wait strategy where they wait for primates to expose themselves into more open areas in the canopy before they attack (Mitani et al, 2001; Shultz, 2001; Boinski et al, 2003). Exposed canopy can leave the monkeys in plain sight of raptors, and vulnerable to attack, whereas vegetative cover across the canopy provides protection and allows them to move through the canopy in relative safety. Cords (1990) found that blue monkeys reduced their vigilance when foliage density increased, thus showing that the monkeys feel safer when the habitat offers increased cover. Cheek pouches can be employed to reduce predation risk (Lambert, 2005). If foraging in a risky area, perhaps with limited canopy cover or foraging on the ground, samango monkeys can fill their cheek pouches with food before moving to a safer area such as a tree with increased foliage density to consume the food item. Vegetation, especially canopy foliage provides much needed cover to limit any aerial attack. However, too much foliage can have negative effect (Boinksi et al. 2003) and can obscure vision and can result in predators being undetected. The lack of significant results for look-ups, scans and total vigilance could be attributed to the fact that the monkeys despite the reduction of cover by nearly 20%.

During the four months of the study, I witnessed only one instance of aerial threat. The ‘ka’ or ‘ka-train’ of the male eagle alarm call (Papworth et al, 2008) was heard and a raptor was observed flying very low, just above the canopy (Eva Muers, pers. obs.). The troop responded to the male call with a chorus of low ‘chirps’ and high ‘grunts’. The male alarm call was heard a further five times. This alarm calling between members of the troop continued for approximately thirty minutes. The monkeys being observed at the food patches on that particular day were an adult female at the ground patch and a subadult at the top patch. When the first alarm call was heard, neither forager responded and continued searching. A few minutes later when they had finished searching and when they did vocalise, it was a low 'grunt'. Their unresponsive behaviour suggested that they were aware of the threat but did not consider it dangerous. It seems likely that these monkeys were foraging in an area in which they perceived to be safe, one with vegetative cover that prevented an aerial attack. As already discussed, the tall forest is the ideal habitat for arboreal monkeys like the samangos due to the extensive canopy cover. The fact that this habitat provides such effective cover means that the monkeys can reduce their vigilance levels when foraging in this forest. The presence of the raptor and the alarm response of the troop demonstrated that the monkeys do consider aerial predation a significant threat. However, the unresponsive behaviour of the observed foragers suggests that there was no imminent danger to them. Therefore, there was no need to cease foraging, either to be vigilant or to move to a safer position in the forest strata.

Visibility

Habitat visibility had no effect on vigilance levels. This contradicts the results found in the Emerson et al (2011) study. A number of studies have shown that visibility is important in primates when managing predation costs. Obstructive cover increases vigilance levels (Treves, 2002). Diana monkeys show an increase in clear calls when habitat visibility is low due to dark or dense vegetation (Uster and Zuberbuhler, 2001). Clear calls in this species are employed primarily to avoid predation. Enstam and Isbell (2004) found that patas monkeys prefer to utilise a tall microhabitat over a short microhabitat. Individuals were frequently observed high up in the trees scanning. Their use of tall trees enhanced their ability to detect predators. Primates are not restricted the ground and can use the increased visibility found higher in the canopy by increasing their height above the ground (van Schaik et al, 1983). One might assume that primates would be more vigilant when in open habitats. Jaffe and Isbell (2009) found that vervets were less vigilant in open areas. Their suggestion was that the monkeys did not need to increase their vigilance levels due to the good visibility. The main predator of vervets in their study was leopards. As leopards hunt by ambushing or stalking their prey, they rely on dense vegetation for a successful hunt (Chase Grey, 2011). Emerson et al (2011) found that GUDs in samango monkeys were significantly affected by blocked sightlines but not by ground vegetation, whereas the present study found no significant effect of visibility. The Emerson study used curtains to block sightlines and the experiment was run for six days. It could have been the novelty of the curtains that caused a significant effect rather than the blocked sightlines. This suggests that either the monkeys do not use clear sightlines when foraging or that the study habitat had good visibility that allowed the monkeys a clear view of their surroundings. I propose that primates do use sightlines when foraging and that it is the habitat characteristics that are the cause for the lack of significant results.

Age/sex class

There was a lack of significant effect of sex on foraging behaviour. However, in white-faced capuchins, *Cebus albifrons* (Rose and Fedigan, 1995), Thomas langurs (Steenbeek et al, 1999) and white-tufted capuchins (van Schaik and van Noordwijk, 1989), males were more vigilant than females. Cowlishaw (1998) found that female chacma baboons were more vigilant than males. The lack of significant results could be due to the lack of males observed at the food patches. Out of the 19 days, I only observed males three times. The majority of the foragers were subadults. This is a surprising result. In samango monkeys, it is the male that gives the eagle alarm call (Ian Gaigher, pers. comm) and therefore should be the more vigilant.

Spatial variation in GUDs

The monkeys show significant spatial variation in their GUDs and seem to perceive a higher predation risk at the three stations located close to the cliffs. Raptors were observed flying across these cliffs, just above the canopy and these aerial predators have also been observed sitting on the cliff edges just above the tallest trees (R. Sassoon, pers. obs.). More specifically, station 4 had the highest GUDs. The eastern side of this station faced the eagle nest and is located in an open patch of forest with exposed canopy and clear visibility. Although the nest has not been in use for some time, the fact that it can be clearly seen visually by the monkeys shows that they could potentially still regard it as a threat. Vegetation can provide cover and protection from aerial predators (Isbell, 1994; Boinski et al, 2003). It could be that despite the highest patches being 5m up, a good distance below the canopy and this station having one of the lowest exposed skyline measurements, the monkeys still experience fear of the open habitat. It seems that they are subject to increased predation risk when foraging from these patches and are responding to the presence of the nest, the open forest and clear sightlines with higher GUDs. However, the monkeys are not responding with increased vigilance.

Behaviour and GUDs

The second objective of the present study was to determine whether the behavioural measures validated the experimental GUD results. To summarise, the monkeys showed a preference for visiting top patches first, decreasing GUDs and increasing conspecific vigilance were found with increasing height. Height did not significantly affect any of the other component behaviours. Decreasing GUDs and increasing conspecific and observer vigilance were revealed with decreasing cover. Canopy cover did not significantly affect any of the other component behaviours. There was no effect of visibility on either GUDs or vigilance behaviour. In this case, vigilance completely match the GUDs and even if significance was not found for either GUDs or behaviour, I would have expected to find similar results. For example, in the case of height, GUDs decreased with increasing height, whereas the one measure of vigilance does the opposite and increases with height. The two measures are clearly detecting different elements of behaviour and further work is clearly needed to determine the degree to which they complement each other.

There are only three studies that have looked at GUDs with behaviour and only one study measuring predation risk using both GUDs and vigilance in the primate literature. Thick-tailed bushbabies revealed higher GUDs and heightened states of vigilance when feeding in riskier patches. These were feeders placed on the ground. However, two studies on ungulates have employed such methods and are worth some discussion here. Both looked at the effect of risky and safe habitats on foraging behaviour by measuring GUDs and vigilance in Nubian ibex (Hochman and Kotler, 2006) and mule deer (Altendorf et al, 2001). Nubian ibex exhibited high GUDs and and high vigilance in riskier patches, whereas mule deer revealed high vigilance at risky patches but this was not confirmed by all GUDs. These studies all measured behaviour in different ways, through the use of cameras and behavioural observations. Only direct behavioural observations that record behaviour at the feeding stations, from the start of foraging until the end and the forager has left the patch, can provide an in-depth and accurate measurement of foraging behaviour. The current study thus extends the approaches that have been attempted in previous work.

Future work

The GUD methods of the present study followed Emerson et al (2011). They were able to determine the optimum volume of peanuts to substrate. This was not possible in the present study and on occasion, the monkeys would deplete the patches to zero peanuts. It would be interesting to observe the monkeys' behaviour if the number of peanuts was reduced, the volume of substrate increased or some sort of cover or obstruction was placed over the tub so that it is not so easy for a forager to search and find peanuts. This would mean the monkeys would have to work harder. This will in turn increase their foraging costs and influence the foraging decisions that they make.

A horizontal landscape of fear has already been generated for this population, showing high and low risk areas of predation risk (Coleman, 2013). The experimental array could be set up in each area and the foraging behaviour compared between the two. This would be the first study to use the GUD approach to confirm an animal's behavioural landscape of fear. Also, Lajuma has another habituated group of samango monkeys. The home ranges of the two troops are different but are adjacent and sometimes overlap, especially in terms of sleeping sites. Both populations also utilise similar habitats within their own home ranges. An experimental array could be set up in each of the home ranges simultaneously, in the same habitat to compare the foraging behaviour of the two troops and determine if there are differences in the foraging costs across populations. Setting two arrays simultaneously will mean direct comparisons can be made and will reduce confounding factors, such as seasonality. Also, one troop is considerably larger (Ian Gaigher, pers. comm). The larger troop could have lower predation pressure and therefore reveal lower GUDs. Comparing GUDs between the two populations would determine if any potential variance could also be attributable to group size. Such a study would make for an interesting comparison.

In conclusion, the use of the GUD technique has proven to an effective tool to measure predation risk in samango monkeys as revealed by their GUDs. The present study confirmed the height effect on perceived predation risk. Applying behavioural observations with the GUDs did not result in validation replication of the results for the experimental approach. Nonetheless, the use of GUDs and behaviour should not be dismissed immediately. The present study has produced some interesting results. The monkeys show a preference for the top patch, which in turn has the lowest GUDs. Height and canopy cover have significant effects on GUDs and vigilance. Hopefully this will result in more GUDs studies in primates in the future.

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