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The effect of predator activity, weather and habitat variation on activity patterns of rock and bush hyrax (Procavia capensis and Heterohyrax brucei) in a mountainous environment

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The effect of predator activity, weather and habitat variation on activity patterns of rock and bush hyrax (*Procavia capensis* and *Heterohyrax brucei*) in a mountainous environment

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Abstract

The relationship between a predator and its prey is multifaceted and this study aims to expand one of the keystone concepts within predator prey interactions. The spatial and temporal changes in a prey animal's behaviour when there is a perceived risk of predation.

Hyrax, a small African mammal, plays an integral role in rocky habitats as a key food source for many predators. The purpose of this study was to test the impact of predation on hyrax using giving-up density (GUD) experiments to establish a landscape of fear. Due to the absence of interaction from the hyrax with the GUD experiments a camera trapping protocol was implemented to collect behavioural data on hyrax in the Soutpansberg Mountains in northern South Africa.

The study aimed to test a number of conclusions made in the literature about hyrax including their classification as a diurnal species, the potential for nocturnal activity and the impact of predation on the diel cycle. Behavioural plasticity with respect to seasonal and environmental changes is also explored including the extent to which they display behavioural thermoregulation.

Hyrax showed nocturnal activity with 8.4% of activity occurring within the dark hours of the 24-hour period but the level of predation pressure may be limiting the level of nocturnality. Hyraxes were also significantly impacted by environmental variables. Activity increased with temperature in all four seasons and rainfall had an immediate effect of reducing activity. It was shown that hyrax demonstrate site specific activity that is consistent over time but can vary within a location.

This study is novel in its methods for studying hyrax and has presented new information on this understudied species that may have far reaching implications for future studies on hyrax and their predators.

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Abbreviations

Hyrax: rock hyrax (*Procavia capensis*) and bush hyrax (*Heterohyrax brucei*)

PPP: Primate and Predator Project

GUD: giving-up density experiment

REM: rapid eye movement

GLM: general linear model

GLMM: general linear mixed-effects model

PTR: Preferred thermal range

Statement of copyright

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Acknowledgments

In keeping with the theme of this dissertation...
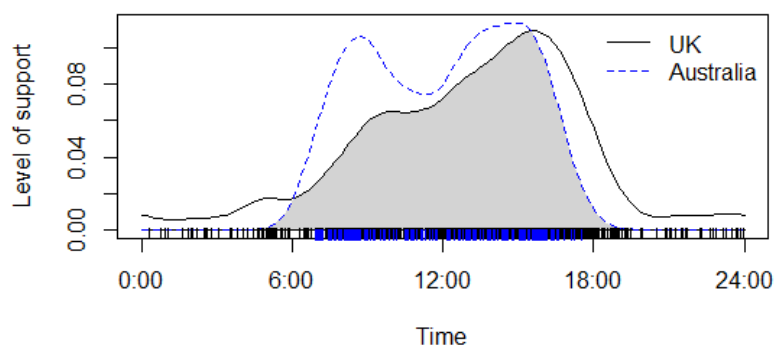
Figure 1: Thanks to my support crews in Australia and the UK for all your love and guidance through this roller coaster of a journey.

Table 1: A break-down of the people who have helped me throughout this journey and where they can be found in their natural habitats.

Site	Team Members	Role	Notes
Durham University	Prof. Russell Hill & Dr. Shane Richards	Supervisors	Thank you for taking me on as a student and for all your guidance
Lajuma Research Centre	Sam and Katy Williams, Caroline Howlett, Andy Allan, Oldrich and Judy van Schalkwyk (Mila & Hazel), Ian Gaigher, Project Assistants and staff at Lajuma	Field station staff and fieldwork support crew	Thank you for keeping me sane, assisting me with fieldwork, making me laugh when I wanted to cry and lending me your shoulders when I did cry
Departments within Durham University	Anthropology postgraduates: special mention to Leah; Biology Postgraduates: very special mention to Claire	Support crew	An amazing bunch of people who I admire and respect and who understand my journey better than most.
Friends	Caroline, Claire, Elinore, Ellie and the YWP crew, Meredith, & Mina	Life support	NB: Team members in alphabetical order (eliminating favouritism). Thank you for being who you are and who I needed you to be during this process.
Family - UK	*Parr /Taylor* spp.	Home away from home	An ear to listen, arms to hug and a bed and a hot meal whenever I needed it.
Family – Australia	*Parr/Lake/Spence* spp.	Bottomless pit of love and support	There are no words, just...Thank You.

Chapter 1 : Introduction

Predation influences animals in a multitude of ways (Lima and Bednekoff, 1999; Verdolin, 2006). These influences can activate short term responses such as the fight or flight reflex of an animal through to long term evolutionary effects where an animal evolves a unique characteristic due to continuous pressures of predation (Seghers, 1974). When exploring the subject of predation, the majority of literature explores only the lethal effects of predation on prey and the wider ecosystem (Schmitz, 1998). However the vast majority of effects are non-lethal and are considered by some to be more important (Cresswell and Quinn, 2013; Lima, 1998a).

Group living is a classic example of an evolutionary anti-predation mechanism (Krause and Ruxton, 2002; Roberts, 1996). One explanation is the dilution effect; an animal is safer in a group than on its own due to the 'many eyes' hypothesis which states that by living in a group each individual can be less vigilant as there is a cumulative effect of vigilance as group size increases (Foster and Treherne, 1981). It also has additional social benefits including increased mate choice as demonstrated by Pereira and Weiss (1991) who observed female ring tailed lemurs (*Lemur catta*) selecting immigrant males in preference to the resident and dominant males.

Another benefit of group living is the confusion effect (Landeau and Terborgh, 1986). When a species group together *en masse* especially when resting means it is difficult for a predator to identify an individual target and make a successful kill. This is especially true when groups of animals are resting and therefore an easier target for predation. Heithaus and Dill (2002) recorded that bottlenose dolphins (*Tursiops aduncus*) rest in deep open water away from their main predator, tiger sharks (*Galeocerdo cuvier*), and that they gather in larger groups when resting than when foraging.

Despite the evolution of anti-predation measures like group living, animals are still vulnerable to predation right across their range. It is how they combat this variation in predation pressure through behaviour change that is the focus of this study.

Landscape of fear

The relationship between a predator and its prey is multifaceted and this study aims to expand one of the keystone concepts within predator prey interactions: the spatial and temporal changes in a prey's behaviour in response to perceived risk of predation. Within recent academic literature the spatial element of this interaction has been given the title of the "landscape of fear" (Laundré et al., 2010). The theory behind the landscape of fear is dominated by the perceived predation risk and the resulting response of a change in density or behaviour of prey species. The predation risk can be mapped onto the landscape as peaks and troughs which represent areas where the prey species perceive high and low levels of threat from predators. These threats can be direct sensory cues such as odours from faeces and urine (Shrader et al., 2008) or they can be indirect cues such as moonlight (Orrock et al., 2004) and vegetation cover (Jacob and Brown, 2000).

The term "landscape of fear" could be seen as misleading as fear has anthropomorphic connotations and is used to describe a wide range of animal behaviours (Boissy, 1995). There are physiological changes within an animal that can be measured as a way of quantifying stress, levels of hormones such as cortisol (Grandin and Deesing, 2002) are commonly used. But behaviours can also be quantified as a way of measuring stress (Rushen et al., 1999). Recent studies by Brown, Kotler and colleagues (2004; 1999; 1999) showed prey animals clearly favoured sites that gave them some form of protection from their predator(s), deeming them "safer" and giving support to the idea that a prey animal sees "fear" of predation as an important factor when assessing its surrounding habitat.

The composition of a landscape of fear is a combination of the complex behaviours of predators and their prey along with their respective population dynamics and ecology (Hernández and Laundré, 2005; Laundré et al., 2001; Laundré et al., 2010). To begin to understand the landscape of fear you must account for conspecific and allospecific interactions. For example, Laundrè and Hernandez (2003) examined the hunting behaviour of pumas (*Puma concolor*) and the association with certain forest types and showed a definite preference by pumas for juniper-piniyon forest type and specifically forest edges. However, the strength of this result was diluted by the observed winter foraging preference of the puma's main prey species, the mule deer (*Odocoileus hemionus*). Therefore, Laundrè and Hernandez (2003) demonstrated a complete view of a landscape of fear is needed to put any behavioural observation into context.

Giving up density experiments as a measure of fear

The classic method for describing the landscape of fear is using giving up density (GUD) experiments (Bedoya-Perez et al., 2013). The method involves the use of artificial food patches that are placed over the landscape in a grid (Druce et al., 2009) or along transects (Makin et al., 2012; Sullivan et al., 2001) or stations with multiple trays at each station (Abu Baker and Brown, 2009; Kotler et al., 2004). These trays are then filled with a food source that is mixed in with an inedible substrate that forces the study species to spend time searching the patch for food (Kotler et al., 2001). The typical outcome of studies into the ecology of fear is the production of spatial maps of the animals predation cost of foraging in a specific area (Brown et al., 1999; Laundré, 2010). This type of method has previously been used to explore the landscape of fear for rock hyrax in the Augrabies Falls National Park in South Africa (Druce et al., 2006; Kotler et al., 1999).

Theoretical Framework

Understanding the influence of fear on animal behaviour has posed a challenge for ecologists because it is unclear how to measure the predation risk an individual animal perceives in a particular environment. The prevailing approach has used foraging theory models that define the cost of predation relative to foraging activity as a mathematical equation for fear (Searle et al., 2008). There are multiple theories that can be applied to the current question, outlined below is an assemblage of theories that support and complement each other and are applicable when answering complex questions on predation risk. Evolutionary game theory is central to the evolutionary and biological theories utilised today. At its core is the premise of 'survival of the fittest' where organisms must evolve to be stronger, more attractive and live longer than their rivals in order to be selected by a mate and give rise to the next generation (Vincent and Brown, 2005).

One of the most important ways an animal can maintain its fitness is in its foraging success. Optimal forging theory attempts to predict how an animal behaves when searching for food. It first appeared when authors MacAuthur and Pianka wrote an article for The American Naturalist in 1966 which was accompanied in the same year by another very similar article by Emlen. Both stated that to date no one had tried to quantify caloric values and consumption times of different foods to the respective roles in an animal's diet (Emlen, 1966; MacArthur and Pianka, 1966). Today many see this theory as outdated and flawed due to its many assumptions although some aspects of it have proved applicable in the field (Perry and Pianka, 1997). Kotler and Brown (1988) added the element

of interference into the optimal foraging framework which accounts for interference experienced by individual species as a way of explaining habitat partitioning.

Following on from optimal foraging theory and Kotler and Browns' addition of interference is the marginal value theory, developed by Charnov (1976) which examines an animal's foraging behaviour in terms of a 'patchy' habitat and how this can be approached by an optimally foraging animal. Charnov developed a model that has been widely adopted and has since given rise to further models that attempt to incorporate greater levels of biological stochasticity into their methodology (Brown et al., 1999). One such model is the Hierarchical Foraging Theory which will be the principle theory applied in the experimental part of this study. The understanding that both prey and their predators belong to their own separate hierarchies underpins this theory. The spatial overlap of these hierarchies highlights the region in which predator prey interactions are likely to have the highest level of predictability. For the prey species, in this case hyrax, for accuracy in assessing the food for safety trade-off the spatial variation in predator risk and available resources, namely food, must be taken into consideration. Searle et al. (2008) suggests that the development of theory supporting landscapes of fear has progressed in isolation from hierarchical foraging theory and that this isolation could have noticeable consequences for the way that experimenters routinely assess the landscape of fear for foraging animals. Taking this into consideration hierarchical foraging theory will be applied with caution to this study, especially when analysing the data, allowing for increased freedom of interpretation and limitation of assumptions.

This theoretical framework culminates in a theory that can be executed using giving-up density experiments. The framework states that in a depletable patch where harvest rate (H) decreases as food consumption increases over time, animals should abandon the patch when the benefits of foraging no longer outweigh the costs. Incorporated into the framework are costs associated with predation risk (P), searching and processing (i.e., handling and digesting) resources from that patch as well as thermoregulatory costs (C) and missed opportunities elsewhere (MOC). The concept is expressed as: H=C+P+MOC (Brown, 1988). These giving-up density experiments consist of artificial patches where a predetermined amount of food is mixed with an inedible substrate which is what causes the energetic and temporal cost of searching to incrementally increase. As a result the quantity of food left by a forager reflects the overall costs of foraging within that time and place (Bedoya-Perez et al., 2013). These giving-up densities have been used in the past to study the landscape of fear in rock hyrax in Augrabies Falls National Park, South Africa (Druce et al., 2006; Kotler et al., 1999). Here they were successful in demonstrating that hyrax favour covered habitats and contributed to the growing body of evidence that hyrax are central place foragers. Furthermore, they showed hyrax demonstrate site specific activity profiles and a bimodal foraging

activity pattern and that behaviour did not correlate with season concluding that predation risk was the driving force behind rock hyrax foraging activity.

Activity patterns and camera trapping

One way to explore animals' behavioural anti-predation mechanisms is to record their activity patterns. To understand these activity patterns and the way an animal uses them to reduce predation risk, the animal must be observed throughout its diel cycle. Recent advances in technology have given ecologists the chance to observe their study species in a whole new way and limit the impact of an observer on the behaviour of the species. These technological advances include camera traps and GPS collars fitted with accelerometers (Kucera and Barrett, 2011; O'Connell et al., 2011).

With individually identifiable animals a capture re-capture method can be implemented when using camera traps which allows for estimates of abundance and density of wide ranging and elusive species (Karanth, 1995; Silver et al., 2004) in a given area, however, the reliability of this method has been called into question (Foster and Harmsen, 2012). Since camera traps were first implemented for the purposes of non-invasive capture re-capture by Griffiths and Van Schaik (1993), camera trapping methodology and technology has evolved to answer many more questions about animal ecology (O'Brien et al., 2003; van Schaik and Griffiths, 1996). More recently the methods for analysing camera trap images and the data they contain has improved and diversified. This has allowed the relationships of predators and their prey and intra-guild relationships to be thoroughly examined (Cozzi et al., 2012; Cresswell and Quinn, 2013; Davis et al., 2010; Ridout and Linkie, 2009). For example Linkie and Ridout (2011) used camera traps to observe the activity patterns of Sumatran tigers (*Panthera tigris sumatrae*) and their prey in Kerinci Seblat National Park, India. They showed strong temporal overlap of tiger activity with muntjac (*Muntiacus muntjac*) and sambar (*Cervus unicolour*). This was in contrast to the foraging theory that tigers should focus on searching for and taking down larger bodied prey that present the least risk and require them to expend the lowest levels of energy. Surprisingly, they found little overlap between tigers and the largest-bodied prey species available, the tapir (*Tapirus indicus*) which suggests that it is not a principal prey species.

This study uses the methodology of overlapping activity patterns of prey species with its predators as well as looking at other environmental factors that could influence behaviour of both predator and prey and make prey species more or less vulnerable to predation.

Activity/risk trade-off

Why an animal chooses to demonstrate certain behaviours at any given time is influenced by many factors (Laundré et al., 2010), but the constant underlying pressure of predation on prey animals undoubtedly impacts on behavioural decisions (Brown et al., 1999). Explaining the frequency and intensity of certain behaviours by measuring fear has been shown in the experiments of Brown (1988), Kotler (1984) and many others (Verdolin, 2006). Some behaviours, such as foraging, are more critical than others and require greater amounts of time allocated to them (Kotler et al., 2010). This trade-off between activities and the risks involved affects the gamut of behaviours some of which are explained below in the context of their significance with respect to predation risk.

Foraging

The behaviour that is most severely impacted by the threat of predation is foraging as hunger dependent risk taking results in anti-predator trade-offs (Houston et al., 1993; Zollner and Lima, 1997). This is because for the majority of prey animals, foraging can be a time intensive activity and must result in the animal successfully consuming the necessary minimum energetic requirements each day (Lima et al., 1985). To combat this some animals have evolved a flexible activity pattern in order to evade predation (Lima, 1998b). Grazers such as antelope are known as diurnal animals, active during the hours of daylight (Manser and Brotherton, 1995; Rahimi and Owen-Smith, 2007). However, they are often seen grazing throughout the night, especially if there is a full moon which produces enough light to aid them in detecting predators (Manser and Brotherton, 1995; Toit, 1993). Within primates, lemur species including *Lemur catta*, *Eulemur falvus rufus* and *Hapalemur meridionalis* have evolved a cathemeral sleep wake cycle that is hypothesised to maximise foraging and minimise exposure to both avian and mammalian predators (Curtis and Rasmussen, 2006; Donati et al., 2013; Eppley et al., 2015). Rodents, a predominantly nocturnal group of animals, also utilise the lunar cycle to aid in lowering the risk of predation whilst foraging (Kotler et al., 1991). For example, oldfield mice (*Peromyscus polionotus*) appear to decrease foraging activity during the full moon phase where the environment is brightly illuminated by moonlight and they are more visible to predators (Orrock et al., 2004). Some species have evolved behaviours that do not require them to alter the time of day allocated for foraging. Sentry behaviour is seen in group living animals and is one or more animals remaining observant for possible dangers such as predators whilst the remainder of the group are less vigilant whilst foraging (Bednekoff, 1997). Sentry behaviour in meerkats (*Suricata suricatta*) is interesting as meerkats do not share prey so the sentinels or guards are at a disadvantage and must compensate for missed foraging opportunities (Tatalovic, 2010).

The relationship between foraging behaviour, predation risk and group dynamics has been studied extensively in many different taxa and the results show much variability between taxa (McNamara and Houston, 1992). Some of this variation may be explained by life history and so can be predicted to some extent (Abrams, 1991). Each assemblage of animals takes a different approach to achieving the energy in/energy out balance whilst limiting the risk of predation (Lima et al., 1985).

Hyrax put themselves at risk of predation for the energetic gains foraging provides but they have been shown to exhibit more behaviours that place them in yet more danger from a wider range of predators (Olds and Shoshani, 1982; Sale, 1970).

Resting and Basking

For prey species resting behaviour is necessary but can also be a response to external stimuli as Dunbar (1996) suggests that it can be broken down into two categories. Enforced resting that is required for digestive and thermoregulatory purposes and uncommitted resting time that, if needed, could be allocated to feeding, travelling or socialising if required. Some species show higher rates of enforced resting than others, this is most likely due to those species requiring more time for recuperation, predator avoidance, digestion and thermoregulation (Herbers, 1981). With observations showing hyrax inactive 95% of the time they could be at the upper end of the scale for necessary minimum enforced resting among mammals and resting may even be an intermediary between an animal being entirely alert and vigilant and sleeping (Sale, 1970).

Basking is typically associated with ectothermic (cold blooded) taxa such as reptiles (Seebacher and Franklin, 2005), however, mammals have been observed altering their behaviour to achieve and maintain their internal body temperature. These can include posturing toward direct sunlight or moving within a habitat to access better conditions and group living species can utilise conspecifics by increasing physical contact to aid in thermoregulation (Terrien et al., 2011). A possible explanation for these behaviours is that it is a response to thermal and dietary stressors and changes in resting time as well as social and postural thermoregulation is required to maintain their internal temperature within their thermal neutral zone (Brown and Downs, 2005; Donati et al., 2011).

Hyrax in the Soutpansberg Mountains

The Soutpansberg Mountains is a land locked mountain range, located between the Kalahari Desert in the west and Kruger National Park in the east (Schwarz and Fischer, 2006). It is the northernmost mountain range in South Africa and was named in Afrikaans after the large salt pans on its western side (Berger et al., 2003). Covering approximately 6,800 km^2 with peaks ranging from 250 m above sea level to the highest peak Mount Lajuma at 1748 m the variation in topography and altitude across small distances have created an extremely varied climate (Mostert et al., 2008). Rainfall across the Soutpansberg Mountains is variable with the north recording an average of 374mm annually and the south up to 1,874mm where mist precipitation can increase that figure to 3,233mm annually (Hahn, 2006).

The Soutpansberg Mountains is a biodiverse region that contains an extensive faunal assemblage that includes 56% of bird and 60% of mammal species native to South Africa the focal animal in this study, two species of hyrax, the rock hyrax (*Procavia capensis*) and bush hyrax (*Heterohyrax brucei*) (Barry and Shoshani, 2000; Chase-Grey, 2011a; Munyai and Foord, 2012; Olds and Shoshani, 1982). Hyraxes have a wide range of predators within the Soutpansberg Mountains including raptors, carnivorous mammals and snakes. Leopards (*Panthera pardus*) are a known predator of all five species of hyrax (Maloiy and Eley, 1992; Milner, 1994; Stuart and Stuart, 1993). Leopards that inhabit mountainous habitats such as the Soutpansberg Mountains are particularly adept at hunting hyrax (Martins and Harris, 2013; Norton and Henley, 1987). Another mammalian predator, the caracal (*Caracal caracal*) is classed as a mesopredator within the predator guild and is also known to prey on hyrax within its range (Avenant and Nel, 2002; Palmer and Fairall, 1988; Turner and Watson, 1965). Other mammalian predators include brown and spotted hyaena (*Hyaena brunnea* and *Crocuta crocuta*) (Skinner et al., 1992; Skinner and Van Aarde, 1981) and black backed jackal (*Canis mesomelas*) although these are among the rarer carnivores within the Soutpansberg Mountains and their dietary preferences when in the Soutpansberg is as yet unstudied. Known avian predators of hyrax that inhabit the Soutpansberg Mountains include the black or Verreaux's eagle (*Aquila verreauxii*) as it's also known and the crowned eagle (*Stephanoaetus coronatus*), however, the impact these two species are having on the hyrax population is only now being investigated (Hill, R. Pers. comm. 2015). Other predators that may have a lesser impact on hyrax and their behavioural patterns are the reptilian guild as multiple species of venomous snakes are present in the area. Egyptian cobra (*Naja haje*) and puff adder (*Bitis arietans*) have both been documented to prey on hyraxes (Turner and Watson, 1965).

Hyraxes have not been studied in the Soutpansberg Mountains and this location and habitat bring together a unique combination of variables which allow new questions to be asked about the

species and its behaviour. Hyrax, a species with a slow life history and small body size, should be behaviourally risk averse as they cannot tolerate a high level of mortality (Olds and Shoshani, 1982). Certain aspects of hyrax ecology do indicate that this may be the case such as short but efficient feeding techniques (Sale, 1966a), however, this is in contrast to overt basking behaviour that places the animal in danger of predation particularly by avian predators (Sale, 1970). Two eagle species, the black or Verreaux's eagle and crowned eagle, alongside the leopard have all been shown to prey heavily on hyrax in southern Africa and yet in many parts of their range their population has been stable over long periods of time despite this predation pressure (Barry and Mundy, 1998; Barry, Chiweshe and Mundy, 2000; Fourie, 1984; Hoeck, 1982; Mbise, 2005). In conclusion, hyraxes are exposed to heavy predation pressure (significant presence in predator diets) and with a slow life history for their body size this should render them highly sensitive to the threat of predation. This makes hyraxes a good study species for assessing the various impacts of predation with respect to its force on a prey species with a complex behavioural profile.

Aims and objectives

The main aim of this study was to investigate the anti-predation behaviour of two hyrax species within the Soutpansberg Mountains, South Africa.

The objectives of were as follows:

1. Investigating what factors determine the spatial landscape of fear in two species of hyrax in the Soutpansberg Mountains.
2. Understanding the extent to which predation risk determines the temporal variation in activity observed in hyrax.
3. Evaluating the activity profile of hyrax with respect to environmental stimuli including lunar cycle, predation, weather and habitat variation.

Thesis outline

This thesis is structured into five chapters. After this introduction, the methodology chapter (Chapter 2) contains descriptive information on the study species and study site in the Soutpansberg Mountains, South Africa, as well as an overview of the sampling methods for both the ecological and behavioural data collection. Attempts to conduct the proposed giving-up density experiments are described, although these were largely unsuccessful; only the camera traps methods provided substantive information for the data chapters. Chapter 3 is an investigation of the sleep wake cycle of the study species and the external ecological factors that could be influencing the use of light and dark hours in the 24-hour period. Chapter 4 examines the impact

of habitat type on the activity patterns of the study species as well as the potential for partitioning of behaviours depending on characteristics of the site. Finally, in Chapter 5 the two sets of results will be integrated in a general discussion and conclusion on their significance regarding hyrax behaviour. Future research directions are proposed.

Chapter 2 : Methodology

Study species

This study was conducted on two species of hyrax, rock hyrax and bush hyrax, which inhabit the Soutpansberg Mountains in South Africa. Phenotypically, hyrax could be grouped with any number of small mammals including rodents, lagomorphs or even marsupials. However, genotypically they have been placed in the clade Paenungulata, which is headed by the largest land mammal, the African elephant (Murata 2003; Springer et al., 1999). This group also includes elephant-shrews also known as sengis (Family Macroscelididae), golden-moles (Family Chrysochloridae), tenrecs (Family Tenrecidae), aardvarks (*Orycteropus afer*), as well as sea cows (manatees and dugongs) (Order Sirenia) and the African and Asian elephant (Family Elephantidae) (Stanhope et al., 1998a, 1998b). This grouping is confirmed by phylogenetic analysis (Springer et al., 1997; Visser, 2013) but is also supported by physiological and life history traits, such as the unusually long life history of hyrax when compared to other mammals its size (Allison and Cicchetti, 1976; Olds and Shoshani, 1982; Sale, 1965b).

Figure 2.1: Rock hyrax photographed at Lajuma Research Centre using a Reconyx Hyperfire H500 camera trap.

Rock hyrax (Figure 2.1) are a medium-sized, terrestrial, diurnal mammal, although there is anecdotal evidence that hyrax are nocturnal and forage on moonlit nights (Coe and Foster, 1972). The average adult female hyrax weighs 3.6 kg and the average adult male weighs 4.0 kg and has a head-body length of 45-60 cm (Olds and Shoshani, 1982). Generally, both males and females become sexually mature at sixteen months of age but do not reach adult size until 36 months (Mendelssohn, 1965). The gestation period for female hyrax has been estimated at between 6 to 8 months (Van der Horst, 1941) (Murray, 1942; Sale, 1965d) (Mendelssohn, 1965) after which they give birth to an average of two to three young (Coe, 1962). Due to the long gestation period, females give birth once a year and this event is timed to occur prior to or during the wet season (Sale, 1965a; Sale, 1965d). However, this varies greatly throughout sub-Saharan Africa and the Arabian Peninsula. The breeding seasons and reproductive cycles as described in Olds and Shoshani (1982) documents wide variation across the African populations with breeding taking place anytime from July to November. Due to the presence of six mammary glands, the female hyrax has a potential litter size of between one and six pups (Wislocki, 1928). The pups are born extremely well developed with eyes open, adult pelage and the ability to jump and climb within days of birth. Young are able to consume solids after only a few days however there is little consensus on when they are weaned, with estimates ranging from six to 10 weeks up to three months (Ilany et al., 2013a). Hyrax are sexually mature at 16 months, with male young dispersing from the colony within 16 to 30 months of age; however, they do not reach adult size and weight until three years of age (Sale, 1965d). The lifespan of hyrax in the wild has been documented to be up to 12 years (Mendelssohn, 1965) but Fourie (1978) suggests that an average of between 108 and 120 months (9 to ten years) is a more realistic lifespan for wild hyrax.

Figure 2.2: IUCN distribution map of rock hyrax (Butynski, 2015b).

The rock hyrax has a widespread distribution throughout sub-Saharan Africa and North East Africa with the exception of the Congo Basin forests and the island of Madagascar (Figure 2.2). The far reaches of its range include the Arabian Peninsula to the north. It is the north eastern sub species of rock hyrax that inhabits the Soutpansberg Mountains (Visser, 2013).

Shortridge (1934) documented digging by hyraxes and Roberts (1951) reported that they are also known to inhabit holes of other animals including aardvark (*Orycteropus afer*) and meerkat (*Suricata suricatta*). This is most often seen in areas where rocky habitats are overpopulated and the animals are forced to find alternate dwellings. Rock hyraxes are predominantly grazers, feeding on grasses 78% of the time in winter and 57% of the time in summer (Hoeck, 1975). They are generalist feeders and are able to consume a wide variety of flora throughout their range. Rock hyraxes have been compared to sheep in their efficiency in grazing but they can consume similar quantities of plant material in much shorter time periods than domestic ungulates. This is achieved by a distinctive foraging technique of using the rear molar teeth to sheer off large quantities of grass that is then quickly macerated and swallowed. Rock hyraxes have been estimated to be able to fill their stomachs after an hour of continuous grazing (Sale, 1966a). Possible explanations for this highly efficient feeding behaviour may be pressure from predation as well as the hyraxes' inability to tolerate exposure to extreme temperatures.

Figure 2.3: Bush hyrax photographed at Lajuma Research Centre using a Reconyx Hyperfire H500/H600 camera trap.

The bush or yellow spotted hyrax is very similar in appearance to the rock hyrax (Figure 2.3), making it difficult to differentiate the species. The bush hyrax is a slightly smaller animal (weighing between 2.3 to 3.6 kg, with a head-body length of 46.5 to 56 cm). Its major phenotypic differences include a more slender build, a narrower skull and a lighter colour to the pelage (Barry and Shoshani, 2000). In contrast to rock hyrax, the bush hyrax has been classed as semi-arboreal due to its foraging behaviour of climbing vertical trunks of trees and balancing on thin branches to browse, although rock hyrax have also been seen to display this behaviour (Olds and Shoshani, 1982; Sale, 1966a). Bush hyrax has a similar distribution to rock hyrax being found throughout sub Saharan Africa, except its distribution extends into the Congo and Egypt along the Red Sea Coast (Figure 2.4). Its presence in the Congo may be due to the existence of dense forest habitat that can only be utilised by bush hyrax as a semi arboreal species. It too is a diurnal mammal but there is documented evidence for activity during moonlit nights and this species has been seen foraging until 21:00 in the Serengeti, Kenya (Turner and Watson, 1965).

Differentiating between rock and bush hyrax can be difficult as previously mentioned the morphological differences can be very slight. This problem was then confounded in this project by the experimental method of camera trapping, the results of which can be difficult to interpret (O'Brien, 2011). As a consequence of these issues both rock and bush hyraxes have been grouped together for all analysis conducted throughout this project.

Figure 2.4: IUCN distribution map of bush hyrax (Butynski, 2015a)

Both species of hyrax share a similar social structure, which allows for the formation of sympatric colonies (Barry, 1994; Barry and Mundy, 2002; Hoeck, 1975; Zimman, 2003) which is documented in the Soutpansberg Mountains (Roberts 1951). This social structure is based around a dominant or alpha male that controls reproductive access to multiple females. Colonies also include juvenile offspring less than 16 months of age (Ilany et al., 2013b; Kotler et al., 1999; Sale, 1965b).

Groups of hyrax, the size of which varies with habitat suitability and carrying capacity, have evolved for many reasons including as an anti-predation mechanism (Barocas et al., 2011; Hoeck, 1989). Despite this, one disadvantage of group living can be social volatility. Rock hyraxes have been used as a model system to test theories of social change and temporal stability of network motifs because their social associations are relatively stable within years but undergo changes between years (Barocas et al., 2011). The changes in social configurations over time reflect reorganisation to maintain strong structural balance with a high frequency of balanced triads within the network (Ilany et al., 2013b). The formation of balanced triads could be the basis for the evolution of sentry behaviour exhibited by hyrax where an adult hyrax acts as "lookout" for the colony as they rest or forage and gives an alarm call when a threat is detected (Druce et al., 2006; Fanson et al., 2011; Kotler et al., 1999).

Hyrax are a vocal animal, especially when threatened (Barry and Shoshani, 2000; Olds and Shoshani, 1982). Vocalisations are a relatively new avenue of study and early results indicate that large parts of the extensive vocabulary are dedicated predator alarm calls (Demartsev et al., 2014). A recent study has shown that hyrax link distinct sounds, equivalent to a syllable, to form long calls, similar to sentences, that can be replicated by its near neighbours thereby creating dialects that are specific to colonies or areas (Ilany et al., 2013a).

Study site

Site description

Field work was conducted over a period of 3 months at the Lajuma Research Centre, located in the western Soutpansberg Mountains, Limpopo Province, South Africa (23°02'17.1"S 29°26'26.5"E) (Figure 2.5). Professor Russell Hill and Professor Ian Gaigher jointly run the field site.

The site contains a vast array of both flora and fauna within a variety of habitats and is unique within South Africa forming part of the UNESCO listed Vhembe Biosphere (Pool-Stanvliet, 2013). This is due to the geography and abiotic conditions allowing for the formation of a variety of microclimates which are able to support this extensive diversity (Willems and Hill, 2009b). The study area within this mountainous region has fragments of both tall and short forest amongst which are dotted rocky outcrops, also known as koppies (Munyati and Kabanda, 2009; Turner and Watson, 1965). Koppies are the focal habitat of this study.

Figure 2.5: Map of southern Africa showing South Africa (dark grey) and the Soutpansberg Mountain range (in red) with the study site of Lajuma highlighted (white arrow).

Climate

The local climate is difficult to classify but it has been described as temperate/mesothermal by Willems (2007) with cool dry winters from April to September and warm to hot wet summers from October to March (Figure 2.6). The mean annual temperature on the site averages 17.1°C, with a mean annual rainfall of 724 mm (Kabanda, 2003; Willems, 2007). Both temperature and rainfall data were collected from the South African Environmental Observation Network (SAEON) weather station at Lajuma Research Centre. The SAEON station at Lajuma Research Centre is an affiliated site of the SAEON network with staff maintaining on-site weather stations and downloading and transmitting the data back to SAEON and its affiliates
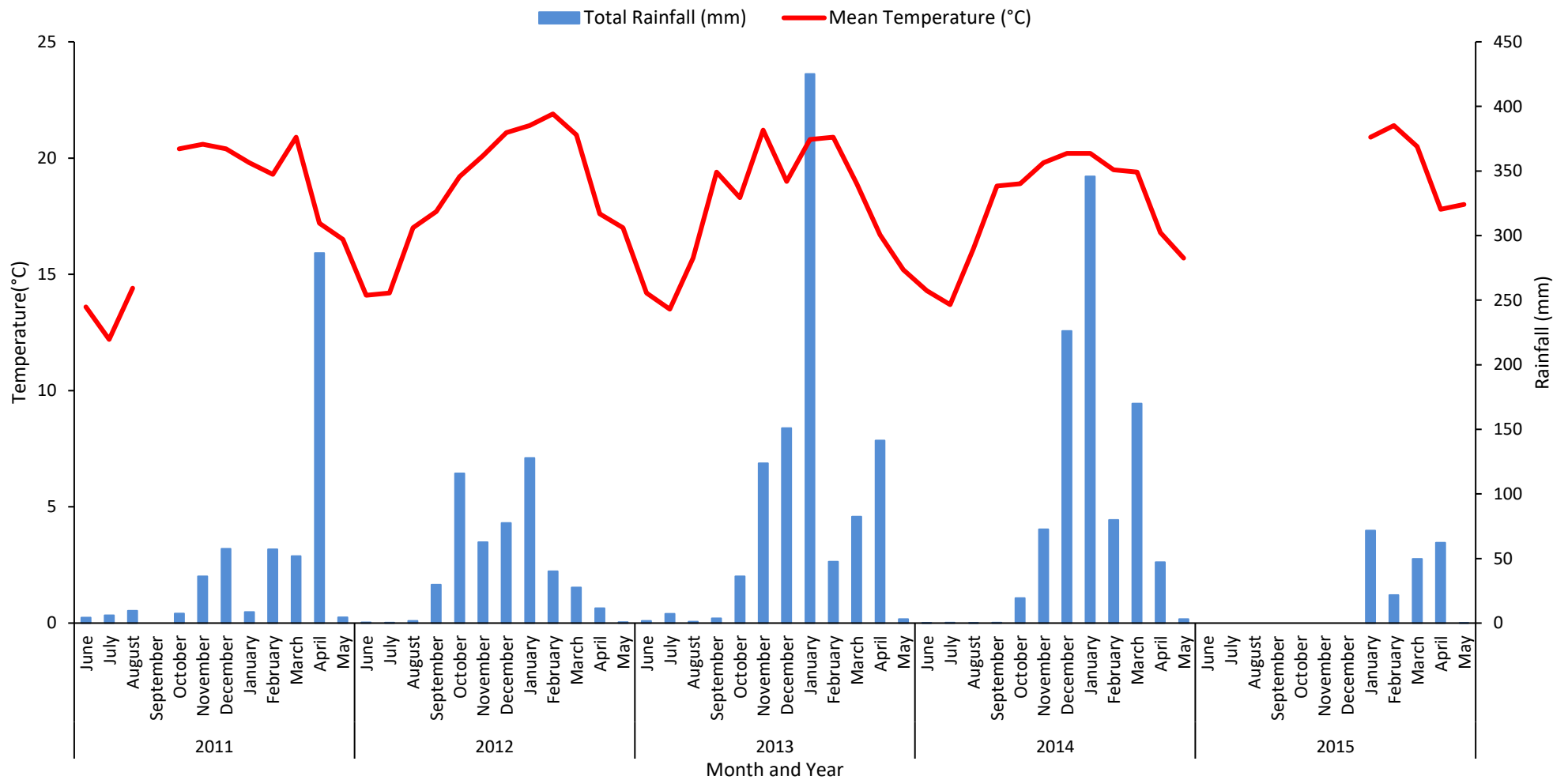
Figure 2.6: Monthly mean temperature (°C) (red line) and rainfall (mm) (blue bars) across 5 years (2011 – 2015) collected at Lajuma Research Centre by a South African Environmental Observation Network (SAEON) affiliated weather station.
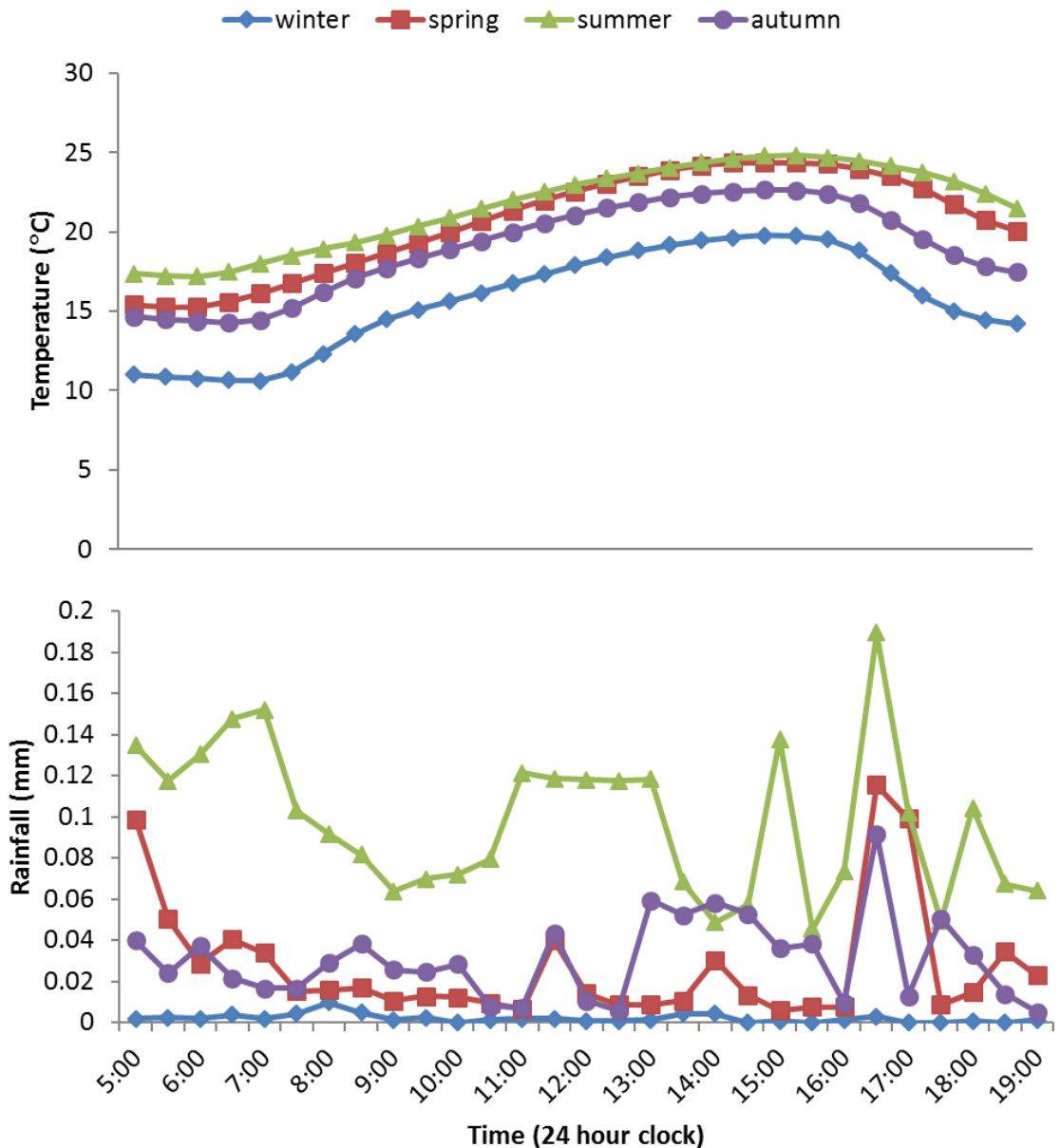
Figure 2.7: Diurnal temperature (°C) (top) and rainfall (mm) (bottom) profiles for the four seasons in the Soutpansberg Mountains, South Africa collected by a South African Environmental Observation Network (SAEON) affiliated weather station over five years (2011 – 2015).

In Figure 2.7 the variation in both temperature (top) and rainfall (bottom) for the hours of daylight can be seen across the four seasons. The pattern of increasing temperature is similar across all four seasons, climbing slowly, climaxing at approximately 15:30 and then slowly decreasing. However, the minimum and maximum temperatures achieved vary greatly from a low of 10°C at 07:00 in winter to a low of 18°C at the same time in summer. The average peak temperature of 23°C measured in summer is 5°C higher than the average high of 18°C recorded in winter. The division of the seasons in the Soutpansberg Mountains can be broken down in two ways. Four seasons of winter (June, July and August); spring (September, October and November); summer (December,

January and February); autumn (March, April and May); or three seasons, cool dry season (winter: May, June, July and August), the wet warm season (summer: November, December, January and February) and transitional periods (March and April, September and October). The temperatures in spring, summer and autumn are highly comparable but rainfall shows greater levels of variability (Figure 2.9) giving weight to the classification of two distinct seasons within the Soutpansberg Mountains with a transition period in between (Hahn, 2006).
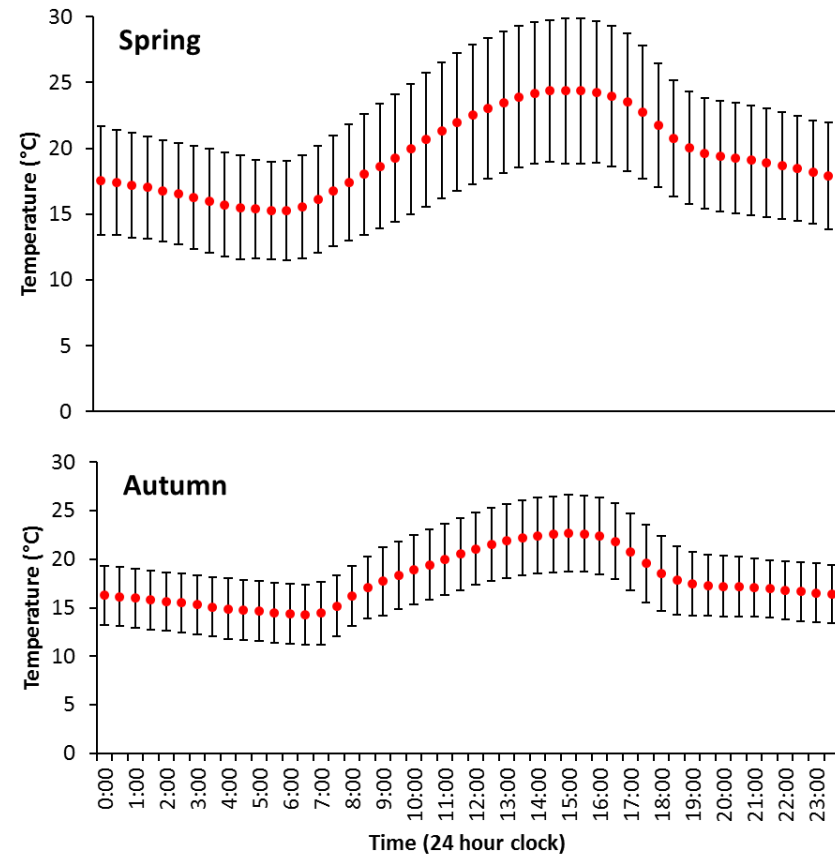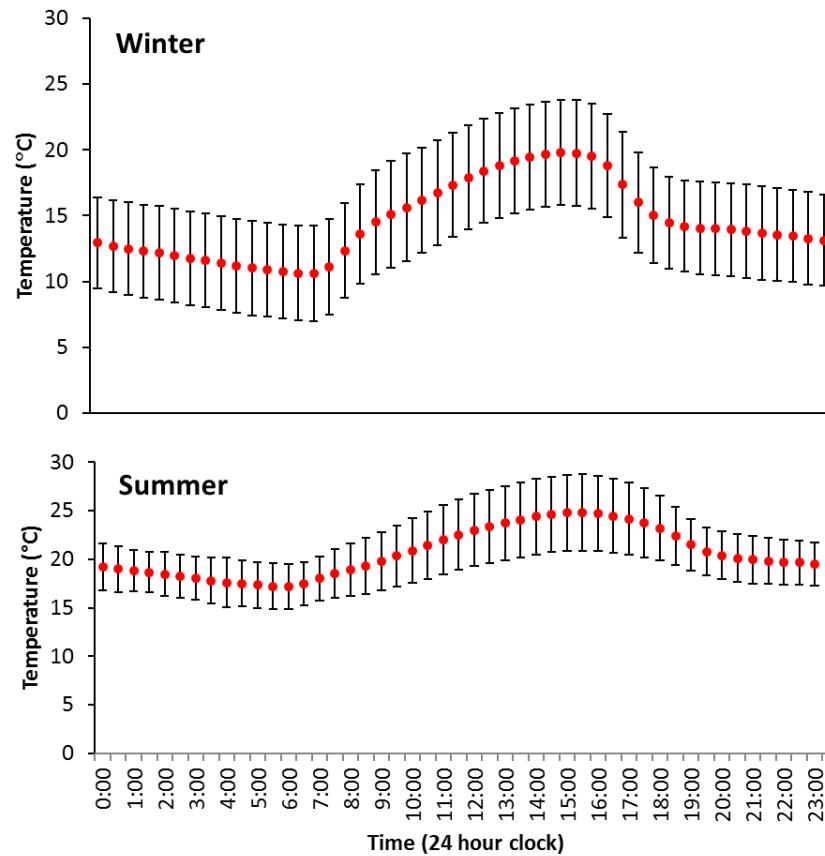
Figure 2.8: Daily temperature profiles for each of the four seasons. Scatter plots with +/- SE showing the average temperature profile in degrees Celsius for the 24-hour period over the four seasons. Data was collected from an African Environmental Observation Network (SAEON) affiliated weather station at Lajuma Research Centre over five years (2011-2015).
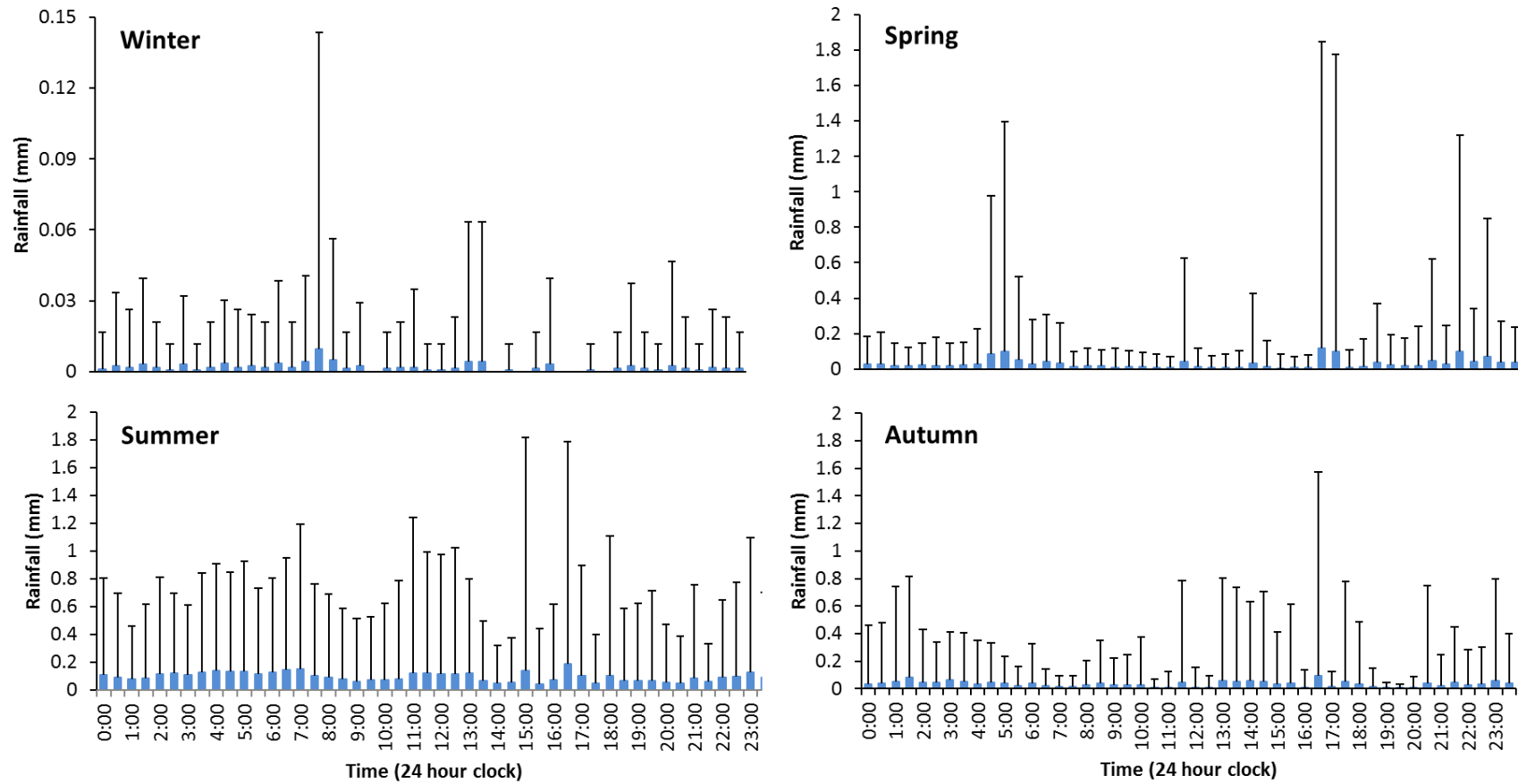
Figure 2.9: Daily rainfall profiles for each of the four seasons. Column plots showing average rainfall in millimetres with +/- SE across the 24-hour period over the four seasons. Data was collected from an African Environmental Observation Network (SAEON) affiliated weather station at Lajuma Research Centre over five years (2011-2015).

Fauna

Predators

There is a healthy diversity of predators in the Soutpansberg Mountains including mammalian, reptilian and avian species (Willems and Hill 2009). Members of all of these groups are known to prey on the rock hyrax (Olds and Shoshani 1982). Known predators of the rock hyrax that can be found in the Soutpansberg Mountains include leopard, crowned eagle, African black eagle, African rock python (*Python sebae*) and puff adder all of which are known to inhabit the study site (Turner and Watson, 1965; Wimberger et al., 2009). The presence of multiple venomous snakes, including black mamba (*Dendroaspis polylepis*), and Mozambique spitting cobra (*Naja mossambica*), also pose a threat. Despite not actively preying on rock hyrax they could cause injury and possible death and could therefore have an effect on range use (Willems and Hill, 2009a).

The mammalian predator guild found in the Soutpansberg Mountains includes one of the highest densities of African Leopard in South Africa (Chase-Grey et al., 2013). Alongside this apex predator is the brown hyaena followed by a number of smaller mammalian mesopredators including caracal, black backed jackal, serval, honey badger, civet and large spotted genet. Although rarer, spotted hyaena, African wild cat, and African wild dog have been recorded in the area (Baker and Brown, 2011; Chase-Grey, 2011b; Willems and Hill, 2009b).

Prey

The prey guild of the Soutpansberg Mountains consists of five species of primate, vervet monkey (*Chlorocebus pygerythrus*), Samango (Syke's) monkey (*Cercopithecus albogularis*), chacma baboon (*Papio ursinus*), lesser bushbaby (*Galago moholi*) and thick tailed bushbaby (*Otolemur crassicaudatus*). Antelope spp. including red duiker (*Cephalophus natalensis*) and bushbuck (imbabala: *Tragelaphus sylvaticus*), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), aardvarks (*Orycteropus afer*), porcupine (*Hystrix cristata*) and scrub hare (*Lepus saxatilis*) are all present in the region. Additionally a variety of small mammals are present including multiple species of mongoose, rodents and shrews (Berger et al., 2003; Stuart and Stuart, 1993).

Pilot study: Giving up density experiments

Locating hyrax colonies

The process of locating colonies of hyrax was conducted in two ways. The primary method was through observation of the animals themselves while walking tracks and game trails. Upon seeing a hyrax in an area, a camera trap (Reconyx Hyperfire H500/H600) was placed in an appropriate location such as on a tree, rock formation or free standing stake facing the location of the sighting to confirm their consistent presence and observe how the hyraxes were using the area. The second method was upon observation of evidence of hyrax habitation then those sites were also monitored using camera traps (Reconyx Hyperfire H500/H600). Evidence of hyraxes included latrines (large quantities of faeces and urine) (Figure 2.10) or environments suitable for hyrax habitation e.g. large rock formations with deep crevices for hyrax to hide and sleep in.

Figure 2.10: Small latrine (faeces highlighted by red circles) located within a koppie in the neighbouring property of Sigurwana; this site was also the focus of a baiting/food trial with peanuts and rabbit pellets visible in the image.

Giving up density experiments

When hyrax sites had been located, an initial trial of the giving up density experimental design was conducted at 2 sites: (1) a walking track along a cliff line where hyrax had often been seen basking, and (2) a cliff edge habitat with a hyrax latrine where animals had been seen (Figure 2.11 and Figure 2.12).

The first of the two sites, the Porcupine trail, had 5 trays set up in a line between the cliff edge and the path with a camera trap positioned directly at the tray. Each tray was formed from the base of a bucket that had been trimmed down to a height of approximately 7.5 cm and a circumference of 43 cm. To begin using the giving up density experiments to investigate how the hyraxes use the environment, the trays were placed in a variety of settings including in the open, near the cliff edge and under bushes and shrubs. The tray was then filled with one litre of sand, sourced from the immediate vicinity and sifted to remove contaminants, mixed with 10 grams of rabbit pellet (a Lucerne based pellet). On the surface of the sand were three indicator pellets used to attract hyrax to the tray and enable quick assessment of foraging activity (Figure 2.11). The trays were covered over each night to prevent foraging by nocturnal animals. As this was a trial to evaluate the experimental design, the timing was flexible so each day the trays were opened at approximately 06:00 (dawn) and closed at approximately 18:30 (dusk). This trial only lasted three days due to interference from chacma baboons.

Figure 2.11: Example of the giving up density experimental design at the Leopard trail.

The second of the two sites, the Leopard trail, had a total of 6 stations set up on and around the cliff edge including next to the hyrax latrine site. The experimental design was the same as the previous trial and trays were again opened up at dawn (approximately 06:00) and closed down at dusk (approximately 18:30). This second trial was concluded after three days due to interference from non-target species (chacma baboons, Cape porcupines and banded mongoose).

A process of elimination was implemented to determine if the lack of activity at the feeding stations from hyrax was due to the experimental design or apparatus, the food or a lack of the study species being present in the area. The initial change involved covering the buckets and placing the food beside the bucket on the natural substrate (rock, soil or sand). This process was repeated for 5 days with no foraging from hyrax observed throughout that time. The trays were then removed completely.

Pre-baiting and food trials

The area surrounding the Leopard trail site continued to be baited with rabbit pellets and whole peanuts with no hyrax activity recorded (see Table 2.1 for duration). For the baiting process, no trays were used. Bait (rabbit pellet and whole peanuts) was placed in small piles (approximately 30 grams of each food type) directly onto the substrate (rock, soil etc.).

Another site was then chosen on a neighbouring property, Sigurwana (Figure 2.12), for a food trial. The site was chosen due to a high level of hyrax vocalisations recorded and the suitability of the environment for hyrax, which had many large rock formations suitable for habitation and areas of grassland and low lying shrubs suitable for foraging. This site was baited with peanuts and rabbit pellets and two camera traps used to monitor the bait and surrounding area. This trial ran for 17 days with a total of seven images from a single visit by one hyrax at one camera.

The final site chosen for a food trial and pre-baiting was a rock formation, the Chimney, on the cliff face adjacent to the Leopard trail (Figure 2.12). A colony of hyrax had regularly been seen in the area. A total of four cameras were placed throughout the rock formation. Two of the cameras were baited with a new food source, a pellet formulated for chickens, which was a predominantly corn based pellet. This site was highly successful in capturing images of hyrax. There was one recorded incidence of a hyrax consuming the bait at this site (a large female rock hyrax that days later gave birth to two young). The site continued to be baited for another week after the feeding was recorded and a tray was placed at the site again to test the giving up density experimental design but no further feeding was detected.

Table 2.1: Breakdown of giving-up density (GUD) and pre-baiting/food trial efforts at various hyrax colonies within Lajuma Research Centre and surrounding properties.

Site	Duration	Bait type
Porcupine trail	3 days (GUD)	Rabbit pellets
Leopard trail	3 days (GUD) 14 days (baiting)	Rabbit pellet and whole shelled peanuts
Sigurwana	17 days (baiting)	Rabbit pellets and whole shelled peanuts
Chimney	33 days (baiting)	Chicken pellets

Camera trapping

Throughout the giving up density, pre-baiting and food trials, a series of camera traps were running at various locations throughout the study site. These cameras served multiple purposes. The initial cameras were erected to confirm the presence of hyrax in certain locations and then throughout the process of fieldwork additional cameras were added as new hyrax colonies and sites were located.

The cameras became an important source of information as the project and the fieldwork progressed. Behaviour and activity patterns of hyrax are informative about many aspects of hyrax ecology including anti predation behaviour and this became of increasing interest when investigating their temporal and spatial activity.
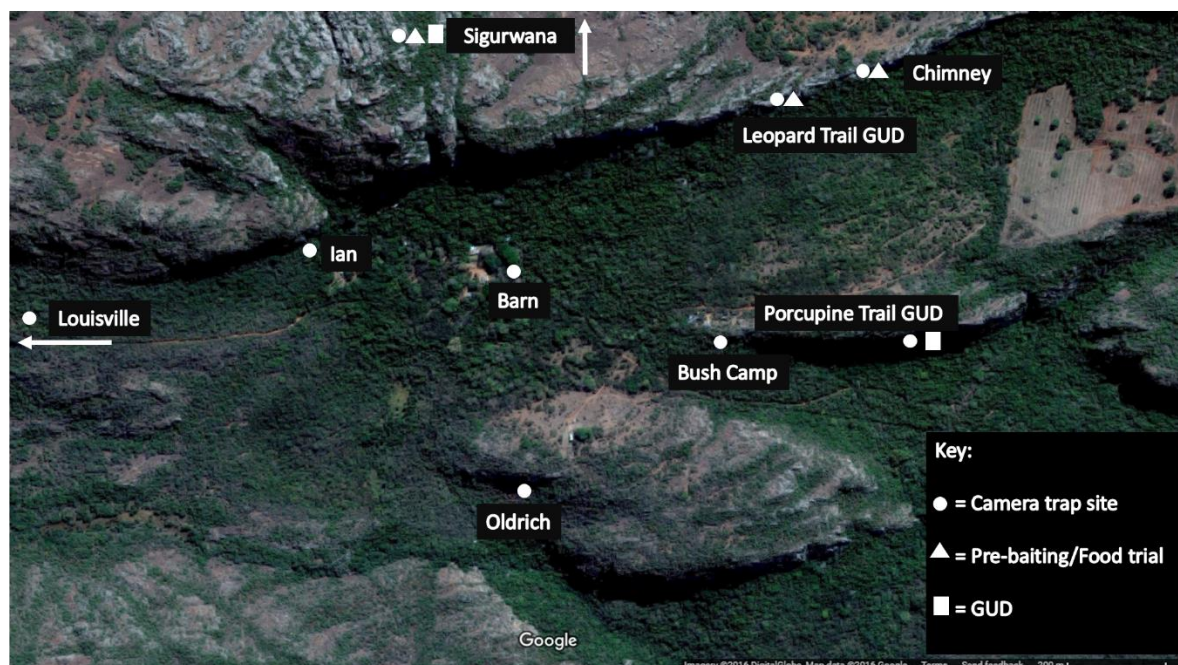
Figure 2.12: Satellite image showing camera trapping, food trial and GUD sites. Satellite image captured 21/10/2016.

Data collection

Camera trapping

Two groups of cameras were utilised for data collection. The first group was erected specifically for this study, as described above. The second group was an established grid managed by a research program, the Primate and Predator Project (PPP), running in the area.

Hyrax cameras

Eight camera stations were set up using a total of 13 cameras (Reconyx Hyperfire H500/H600), to capture hyrax behaviour (Figure 2.12). These stations covered a wide range of habitats including cliff faces, woodland, koppie and road. These cameras captured 6,174 images of hyrax over 79 days. Once the images were downloaded off the memory card contained within the camera trap they were sorted based on the content of the image. If a hyrax was identified by eye in the image it was retained. If a positive ID could not be confirmed the image was discarded.

Table 2.2: Locations and site descriptions for hyrax cameras.

Site	Camera	Site Description
Louisville	Attached to a small shrub	A roadside location that had previously been used by the PPP as a camera trapping location for predators.
Oldrich	Attached to a tree	One camera facing a cliff on the periphery of a piece of land that has been developed with a house and garden. This site had almost constant human activity from the residents of the house and people working with the PPP who constantly frequented the area when following troops of primates as well as domestic animal activity from two resident dogs.
Ian	Attached to trees	A cliff face/woodland site that was on the periphery of a property that housed people and domestic animals and was frequented regularly by troops of both baboons and Samango monkeys.
Chimney	Attached to rocks, trees and stands formed from sticks and rocks	A rock formation consisting of boulders at the top of a cliff face, located on a trail heavily frequented by people and other animals. This site was also used for a food trial and had four cameras.
Leopard Trail	Attached to a tree and a stand formed from sticks and rocks	Adjacent to the Chimney, at the top of the same cliff face, this site was most frequently used as a sleeping site by a troop of baboons.
Sigurwana	Attached to stands formed from sticks and rocks	A site in a neighbouring property, which had small rock formations interspersed in grassland. It is a privately owned property used for tourism with many introduced species of game.
Barn	Attached to a tree and a fence	A group of buildings surrounded by semi-landscaped garden (trimmed grass); a cliff face and bush (see Figure 2.12 for exact location within field site). The hyraxes that inhabit this area are semi habituated due to the permanent human presence. This is also core Samango monkey territory making it an unsuitable site for the giving up density experiment due to interference from the primates. However, it is an interesting site for camera trapping for behavioural and site use study due to the possible inter species interactions.
Bush Camp	Attached to a tree	A cliff face located directly below the main accommodation site for the Primate and Predator Project. This site was frequented regularly by both troops of primates and people.

Table 2.3: Description of active period for all hyrax cameras

Station	Cameras	Active Period	Active Period (Hours)	# Active Days	Habitat type
Louisville	1	08/03/2015 – 17/05/2015	Start: 1100 End: 1000	23+30+17=70 days	Road
Oldrich	1	07/03/2015 – 21/05/2015	Start: 0900 End: 0900	24+30+21=75 days	Cliff
Ian	2	04/03/2015 – 22/05/2015	Start: 1700 End: 1600	27+30+21=78 days	Woodland
Chimney	4	17/04/2015 – 20/05/2015	Start: 1200 End: 1400	13+20=33 days	Cliff
Leopard Trail	2	05/03/2015 – 20/05/2015	Start: 1000 End: 1600	26+30+20=76 days – 2 days lost to card errors = 74 days	Cliff
Sigurwana	2	01/04/2015 – 17/04/2015	Start: 1000 End: 1000	17 days	Koppie
Barn	2	04/03/2015 – 22/05/2015 (Fence) 14/04/2015 – 22/05/2015 (Fig Tree)	Start: 0900 End: 1600 (Fence) Start: 1500 End: 1600 (Fig Tree)	27+30+21=78 days/16+21=37 days	Woodland
Bush Camp	1	20/03/2015 – 19/05/2015	Start: 1600 End: 1000	11+30+19=60 days	Cliff

Primate and Predator cameras

This camera grid was established in early 2011 primarily to monitor the mammalian predator population within the Soutpansberg Mountains. The grid is formed of multiple pairs of cameras placed on or near roads (Figure 2.13), with stations a minimum of 2.75 kilometres apart to reflect the minimum home range of leopards (Mizutani and Jewell, 1998). The pairs of cameras were attached to trees or stakes approximately 30 to 40 cm above ground on opposite sides of the road. The layout of the grid has been altered over the years due to changes in access to land and movement patterns of study species therefore, Figure 2.13 shows all camera locations, some of which are no longer active but from which data is featured in this research.

The cameras were checked, including changing batteries, changing SD cards and clearing the vegetation from around the camera, approximately every two weeks. The images were downloaded off the SD cards and examined using Microsoft Photo Gallery. All images collected were tagged with the information of the animals (species common name) or objects (vehicle, human, bird etc.) captured in the image. The images were then stored in an image library for future use.

Despite this grid being primarily designed to capture images of the predator population it can be useful for estimating the surrounding prey population. However, certain smaller prey species such as hyrax are less reliably recorded due to the location and position of the cameras and layout of the grid. Nevertheless, to collect as much data as possible on hyrax the image library from all cameras, past and present, within the PPP grid was searched for images of hyrax. A total of 4193 images were collected from 24 cameras (12 sets of two cameras). This data set extends from July 2011 through to the middle of May 2015, the end of the field season for this study.

As seen in Table 2.4 there is a significant difference in data quantity depending on camera location. All PPP cameras are located on roads or game trails, as many predators choose the path of least resistance and therefore show a preference for travelling on roads or game trails (Benítez-López et al., 2010; Davis et al., 2010; Dickson et al., 2005; Martins and Harris, 2013; Whittington et al., 2005). This meant that the majority of PPP cameras had very little hyrax activity with the exception of one station (Station 18a) which was decommissioned in early 2014. The Louisville station (part of the hyrax camera array) which was activated for the current study, was placed in approximately the same position as PPP Station 18a.
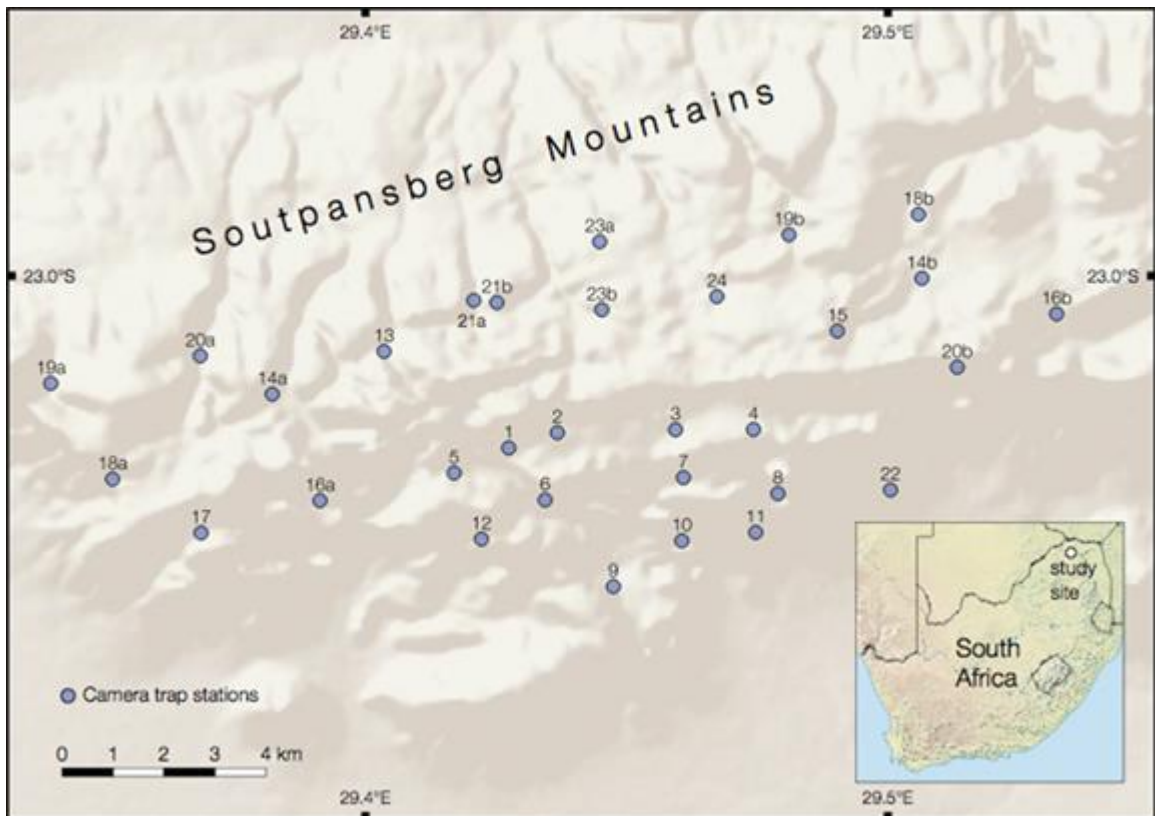
Figure 2.13: A map showing all PPP camera locations including Station 18a in Louisville.

Table 2.4: Breakdown of data collected from all cameras within the current study and from the Primate and Predator Project image library.

Hyrax Stations	# Images	PPP Stations	# Images
Barn – Fence	1080	Station 2	9
Barn – Fig Tree	121	Station 6	1
Leopard Trail	43	Station 7	1
Bush Camp	426	Station 11	3
Sigurwana	7	Station 12	18
Chimney – KSW14	483	Station 14	73
Chimney – KSW16	410	Station 18	3753
Chimney – KSW18	3175	Station 19	4
Chimney – KSW19	21	Station 20	28
Oldrich	98	Station 21	160
Ian	31	Station 23	24
Louisville	279	Station 24	119

Tagging images with behavioural data for analysis of activity patterns

Additional information was added by tagging the images in the image viewing software Windows
Live Photo Gallery. These tags were then exported with the metadata (information attached to

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individual images including date, time, temperature and lunar phase) using ExifTool (Harvey, 2016). By tagging images extra information summarising the contents of the image was added to the metadata. This included the number of animals, their life stage, and the behaviour seen and the number of animals participating in the behaviours (Table 2.5).

All raw data collected during the procedures described above was collated and stored in spreadsheets and workbooks within Excel and all statistical analysis was conducted in R (R Core Team, 2014).

Outline of statistical analysis

The majority of the analysis for chapter 3 was conducted in Overlap (Meredith and Ridout, 2014), an R package that specialises in the analysis of camera trap data. Overlap was used to calculate the density of activity across the 24-hour period for hyrax and their mammalian predators. These data were used to ask questions about the impact of predator activity patterns on density of activity of hyrax. In order to make decisions about the type of analysis appropriate for asking the questions posed in chapter 3 initial tests including Shapiro-Wilks test for normality were conducted. The majority of the data were not normally distributed, meaning non-parametric tests were required for analysis. The Mann Whitney U test was used to test for differences in density of activity of hyrax and their predators with respect to lunar phase and day length. When looking at the impact of a predator's activity density on hyrax density of activity, a Spearman's rank correlation was used.

Chapter 4 analysis centred on behavioural data obtained from the camera trap images. Initial analysis of the effect of weather on density of activity of hyrax across the four seasons was investigated using Pearson's correlations. The influence of rainfall on hyrax density of activity was examined by quantifying activity of hyrax in relation to rainfall, whether rain fell that day, and tested using a Mann-Whitney U test of differences. General linear models and general linear mixed-effects models, implemented using R, were used to analyse the effect of temperature and rainfall on density of activity of hyrax. Analysis in this chapter ends with the use of the Overlap package within R to compare the density of activity of hyrax in differing habitats.

Table 2.5: Explanation of code used for tagging behaviour in camera trap images.

Information	Symbol	Number of individuals	Description of category
Animals			
Adults	A	00	Hyrax over 16 months of age
Juvenile	J	00	Hyrax between 10 weeks and 16 months of age
Young	Y	00	New born hyrax < 10 weeks of age
Behaviours			
Basking	B	00	Hyrax is stationary in direct sunlight; as described by Sale (1970) as solitary resting
Resting	R	00	Similar to basking however the animal is not in direct sunlight
Foraging	F	00	Hyrax seen with food in their mouth
Travelling	T	00	Hyrax seen to be moving past the camera
Socialising	S	00	Grooming, heaping (Sale, 1970), huddling (Sale, 1970), playing (young) and fighting; all grouped together as socialising

Chapter 3 : Activity cycle of two hyrax species in the Soutpansberg Mountains, South Africa

Introduction

Most animals 24 hour sleep-wake pattern can be classified into one of four categories: diurnal, cathemeral, crepuscular or nocturnal (Ashby, 1972; Curtis et al., 2006). Ranging from strict diurnality (active only during daylight hours) to strict nocturnality (active only during hours of darkness) these categories are a human construct to allow comparison of activity patterns within the animal kingdom (Curtis and Rasmussen, 2006). Therefore, the categorisation is on a sliding scale and includes crepuscular animals (active during dawn and dusk) and cathemeral animals (active during both light and dark periods) (Hall et al., 2012). Sleep is best studied in mammals resulting in a myriad of different sleep patterns being observed.

Total sleep time in mammals ranges from four up to 19 hours with rapid eye movement sleep (REM sleep) the deepest form of sleep, occupying between 10% and 50% of that time (Zepelin et al., 2005). The daily activity rhythm or circadian rhythm sets a mammal's sleep-wake cycle (Reppert and Weaver, 2002). The control of a mammal's sleep-wake cycle is in the gene expression by a master clock within the hypothalamus of the brain (Pevet and Challet, 2011). Changes in a mammals sleep-wake cycle occur when the expression of these genes changes (Challet, 2007; Oster et al., 2002). Light is the most powerful trigger of the circadian master clock (Reppert and Weaver, 2002).

Challet (2007) explains that in the majority of cases stimulation occurs through the initial detection of light via the retinal ganglion cells that respond by producing melanopsin. Melanopsin activates the retinohypothalmic fibres which communicate directly with the suprachiasmatic nucleus (SCN) which houses the master clock, within the hypothalamus of the brain. However, Challet also stipulates that there must be some functional differences within the retina of nocturnal and diurnal animals to aid in the regulation of nocturnality and diurnality respectively as there is evidence that when melanopsin production is blocked in mice they can partially switch their activity from night time to daytime (Challet, 2007).

Wollnik et al. (1995) demonstrated that within the SCN if two mRNA transcription factors, c-Fos and JunB are blocked then light induced phase shifts of the circadian rhythm do not occur. Without any chemical interference, it is possible, under laboratory conditions, to reset the master clock and cause a nocturnal species to become diurnal and vice versa. This is done by housing animals with a particular sleep-wake cycle in their optimal condition i.e. diurnal animals in continual light and then introducing periods of complete darkness lasting several minutes to several hours. However, this

process is most effective when conducted on nocturnal species during the dark (active) period (Challet, 2007).

One of the adaptations to diurnality in mammals is the ratio of photoreceptive cells within the eye. Peichl (2005) describes the ratio of cone and rod cells differs between diurnal and nocturnal species with diurnal mammals having a higher cone to rod ratio when compared to their nocturnal counterparts. Cone cells require higher light levels to operate effectively and so are adapted for photopic or daylight vision whereas rod cells are more light-sensitive and better for night, or scotoptic vision. As would be expected, crepuscular and cathemeral species have a more equal ratio of cone and rod cells as both cell types work effectively in medium light. Diurnal species have more cone cells relative to nocturnal species which have comparatively more rod cells (Peichl, 2005). This difference is likely to occur between the diurnal rock and bush hyrax when compared to the nocturnal tree hyrax but there has been little to no research to date on hyrax vision and eye morphology. Millar 1973 describes a light shielding structure within the eye of rock hyrax they may have evolved to prevent damage occurring when hyrax stare directly into the sun whilst on the lookout for aerial predators. There have been studies on the vision of close relatives of the hyrax such as manatees (Newman and Robinson 2006) however a comparison or extrapolation of these findings to apply to hyrax is unlikely in such a diverse group as Afrotheria. Sale 1960 documents anecdotal evidence of hyrax showing signs of good long distance vision but poor vision across short distances. Sale and other authors cite a field guide by Austin Roberts published in 1951 stating the eye structure of hyrax is remarkably different to that of other mammals (Roberts, 1951). Within the field guide by Roberts (1951) there is a reference to a study which has revealed that the eyes of rock hyrax differ entirely from those of other animals but that result is unpublished.

Food availability, feeding schedule and calorie intake have also been shown to affect the master clock, specifically a chain reaction that occurs when food availability and/or calorific intake is reduced (Froy, 2007). These actions prompt changes in activity, such as nocturnal animals becoming active during the day. This is due to a series of metabolic cues that effect the master clock and its synchronicity to light (Challet, 2009).

It is unclear why animals are not active during the entire 24-hour period and what makes an animal nocturnal or diurnal if the physiology of an animal supports flexibility in its sleep-wake cycle. The answer could lie in the synchronous evolution of sleep and endothermy in mammals and birds, which has been well studied and could explain the partitioning of nocturnality and diurnality (Siegel, 2005). Within endothermic mammals, the relationship between diet and sleep is a sliding scale where carnivores have the highest amounts of sleep in the 24 hour cycle followed by omnivores with herbivores demonstrating the lowest amounts of sleep (Siegel, 2005). It has been hypothesised that herbivores have had to reduce the amount of sleep required based on body mass. This could

be due to their position within the trophic cascade as a large proportion are prey species confounded by a time intensive feeding strategy of grazing or browsing with a subsequently long digestive process (Capellini et al., 2008; Siegel, 2009). It is the interaction between mammalian physiological and neural systems, the solar cycle and the food-energy cycle that combine to control the sleep-wake cycle.

Bider (1968) examined animal behaviour and classed the effects he observed into four categories: annual, seasonal, meteorological and climatic. The main annual factors influencing level of activity was the size of the population. Seasonally the factors increased to include reproduction and dispersal, migration and feeding. Meteorological factors are large scale weather events and climatic factors are weather events on a smaller scale. These interactions have more recently been grouped into proximate and ultimate factors with Donati et al. (2009) showing that for cathemeral lemurs the ultimate factors effecting behaviour are thermoregulatory benefits, antipredator strategies, avoidance of competition and metabolic dietary related needs (Santini et al., 2015). The activity pattern of badgers (*Meles meles*) in Bialowieia Primeval Forest, eastern Poland were studied to determine the ultimate factors affecting their circadian activity patterns with shortage of the optimal food source of earthworms in winter the only limiting factor to their circadian activity patterns (Kowalczyk et al., 2003).

Some species within an order will show differences in their sleep-wake cycle and one such group is Hyracoidea. There are five extant species within this order; tree hyrax (*Dendrohyrax* spp.) of which there are three species (*D. arboreous, D. validus, D. dorsalis*), bush hyrax (*Heterohyrax brucei*) and rock hyrax (*Procavia capensis*). Tree hyraxes are strictly nocturnal (Jones, 1978; Milner and Harris, 1999; Sale, 1960; Topp-Jorgensen et al., 2008), in contrast bush and rock hyrax are classified as diurnal (see Chapter 2: Methodology - Study species). The studies of rock and bush hyrax activity patterns in the wild have focused on diurnal activity resulting in an absence of reporting of hyrax behaviour during dark hours (Barry and Mundy, 1998; Barry et al., 2014; Brown and Downs, 2007; Fourie, 1984; Hoeck, 1989; Sale, 1965a; Sale, 1960, 1965b, c; Sale, 1965d; Sale, 1966a, b, 1970); therefore, to date, there is no evidence from wild populations evaluating the occurrence of nocturnal activity.

Studies on wild rock hyrax in a laboratory environment have revealed possible flexibility in their diurnal sleep-wake cycle. Gravett et al. (2012) showed that when wild caught hyraxes were placed in a laboratory environment their use of light and dark hours was considerably different to that suggested by observations in the wild. They recorded the hyraxes as awake for approximately 16 hours per day and that more of the waking phase, including feeding behaviour, occurred in the dark periods. Therefore, they classified hyraxes as polycyclic as they were neither strongly nocturnal nor diurnal. Furthermore, hyrax were recorded to have very low levels of REM sleep with potentially

the lowest proportion of REM sleep seen in any mammal studied to date (Gravett, 2011). An unanswered question, therefore, is whether bush hyrax and rock hyrax in the wild show similar activity patterns to those seen in captivity and whether previous reports of strict diurnality have resulted from a failure to observe the species throughout the 24-hour cycle. REM has been shown to be negatively correlated with predation risk (Lesku et al., 2006). Allison and Cicchetti (1976) modelled both sleep duration and type along with a host of other physiological and ethological variables for 39 mammals including two species of hyrax. They revealed that the gestation period was negatively correlated with REM sleep, indicating that the hyrax could be under more pressure than other small mammals of similar body size due to its unusually long gestation period.

The evolution of an animal's sleep-wake cycle can be influenced by many factors such as the lunar cycle, the climate, habitat and for prey species, the risk of predation (Lesku et al., 2006; Zepelin et al., 2005). Allison and Cicchetti (1976) reported that hyrax have a danger factor of around 0.5. This figure is calculated from both ecological and physiological factors. These include: life span measured in years; body weight measured in kilograms; brain weight measured in grams; gestation measured in days; a predation index (on a scale of 1 to 5, with 1 being a heavily predated species); sleep exposure (on a scale of 1 to 5, with 1 being a maximum exposure to predation whilst sleeping); overall danger (on a scale of predatory danger from 1 to 5, with 1 being low risk of predatory danger) and the proportions of different types of sleep seen in the species. The scaled factors were concluded from field observations. Allison and Cicchetti (1976) modelled multiple physiological variables along with two types of sleep. Overall danger and gestation accounted for 66% of the variability in REM sleep. A negative correlation between gestation and REM was shown not to be influenced by any other variable. Certain animals, including hyrax and guinea pigs, have unusually long gestation periods when compared to their body weight which could be evidence for the negative relationship between REM and gestation period. Therefore, the relationships between REM, overall danger and gestation all point toward REM sleep being disadvantageous to heavily predated species such as hyrax (Barry and Barry, 1996; Chase-Grey, 2011a; Fitzgerald, 2015a; Milner and Harris, 1999).

The hyraxes heavy level of predation does not compare with a danger factor of 0.5 when compared to other similar sized heavily predated species, such as rabbits which are allocated a danger factor of 1.75 in Allison and Cicchetti's analysis. Three species of hyrax (*P. capensis, H. brucei and D. validus*) are grouped together in the centre of a plot of danger factor against size factor (hyrax all score approximately 0.2 in size factor) below two clusters of heavily predated animals including domestic animals (goat (*Capra hircus*), sheep (*Ovis aries*), cow (*Bos taurus*) and horse (*Equus caballus*)) and African savannah primates (vervet monkey, patas (*Erythrocebus patas*) and baboon (*Papio* spp.)) that all have a danger factor of greater than one and a size factor of between 0.5 and

1.5. This demonstrates that ethological rather than physiological factors may have a greater influence on hyraxes' total sleep time.

Here I investigate the 24-hour sleep-wake cycle of the hyrax population in the Soutpansberg Mountains, South Africa, based on camera trapping. Camera trapping as a non-invasive method for studying animals in their natural habitat has been rapidly developing over the past few decades and is now considered one of the best ways to capture large amounts of detailed information about a species whilst causing minimal disruption to its natural behavioural patterns (O'Connell et al., 2011); this method is particularly useful for gathering information during times when the animals cannot be physically observed by humans, as is the case with this study.

When investigating the potential for nocturnal activity in hyrax it is clear that there are positive indicators of potential for nocturnal activity. The ethological factors include type of sleep with hyrax showing low levels of the deeper REM sleep as well as sleep duration at the lower end of the spectrum for endothermic mammals. The main physiological factor is the potential for adequate night vision on moonlit nights as concluded by eye morphology and as a diurnal mammal the arrangement and ratio of rod and cone cells within the retina.

Day length

Day length impacts the majority of terrestrial animals irrespective of their location and or sleep-wake cycle (Hediger, 1980; Helm and Gwinner, 2006). Within the year, due to the seasonal nature of climate and light patterns, terrestrial animals must compensate for those periods where conditions are suboptimal and take advantage of the times when conditions are most favourable. The changes in day length have a greater effect on strict diurnal and nocturnal species as they must conduct all essential tasks in hours of light or dark respectively (Ashby, 1972). Cathemeral and crepuscular animals are under less pressure due to their ability to utilise both light and dark hours (Tattersall, 1987, 2006). Day length has a significant impact on the daily activity patterns of diurnal chacma baboons in South Africa (Hill et al., 2003). During the winter months, baboons showed a significant decrease in time spent resting which was related to decrease in day length and a subsequent reduction in unallocated time. Day length seems to have a similarly significant effect on the cathemeral redfronted lemur, *Eulemur fulvus rufus*, with total and diurnal activity increasing during the austral summer (long days) and nocturnal activity increasing during the winter (longer nights). Furthermore, irrespective of season, the lunar phase had a significant effect on the distribution of activity across the 24-hour cycle, with most nocturnal activity recorded during parts of the night with greatest brightness (Kappeler and Erkert, 2003). Evidence from both species could

indicate that day length has a significant effect on activity patterns and that effect is independent of the animal's diel cycle.

In addition, some species have more complex physiological constraints placed upon them due to the seasonal variations in quality and quantity of food and fluctuations in temperature (Fernandez-Duque, 2003). Both food shortages and lower temperatures can affect hyrax. However, the temperature is likely to be more of a limiting factor due to hyraxes' inability to adequately maintain their internal body temperature (Sale, 1960).

This study aims to investigate if hyraxes show changes in activity pattern across the seasons. It is hypothesised that if nocturnal activity is detected it will be highest during winter when temperatures fall and food availability and quality is at its lowest.

Hypothesis:
H_0: Day length had no impact on the 24-hour activity cycle of hyrax in the Soutpansberg Mountains.

H_1: Nocturnal activity was greater during winter when compared to summer due to the shorter day lengths in the winter period.

Lunar cycle

The lunar cycle gives cues that can be recognised and used by animals to initiate or terminate certain behaviours such as reproduction (Dixon et al., 2006), foraging (Trillmich and Mohren, 1981) and predation (Kotler et al., 2010). Many species of frog spawn during the full moon as this helps increase the visibility of the male's colours and behaviours to the females (Grant et al., 2009). Nocturnal insectivorous birds, such as Nightjars (*Caprimulgidae* spp.) show increased activity during moonlit nights as their chosen prey is more active during the full moon phase (Jetz et al., 2003). Many mammals, including bats (Lang et al., 2006) and seals (Horning and Trillmich, 1999) also show behaviour changes on a full moon. White-throated round-eared bats (*Lophostoma silvicolum*) increase time spent actively hunting whereas seals come ashore in greater numbers during the full moon. Those that remain at sea dive deeper when hunting as their prey stay lower in the water body to avoid detection in the well-lit upper layers of water.

It has been hypothesised that this variation in activity patterns within primates and other mammals could be due to the constraint of predation limiting species that are physiologically capable of nocturnal activity from showing such behaviour (Hill, 2006b). In contrast, lemurid genera of primates including *Hapalemur*, *Eulemur* and *Lemur* spp. all exhibit cathemerality and lunarphilia (increased activity during increased moonlight) (Eppley et al., 2015). The long term presence of cathemerality within *Eulemur* species has been confirmed by Kirk (2006) who describes the eye morphology as similar to other cathemeral mammals. Kirk (2006) suggests that cathemerality is

most likely an ancient trait within this group, present in the last common ancestor (Donati et al., 2013; Kirk, 2006).

However, predators themselves show variation in their activity patterns in line with the lunar cycle (Hayward and Slotow, 2009). This is especially true in areas where there is an established predator guild. Okavango Delta Cozzie et al. (2012) suggest that segregation occurs between the larger and more dominant lion and hyaena and the smaller wild dog and cheetah. They hypothesised that the nocturnal activity pattern of the wild dog and cheetah is starvation driven. They observed that the animals increased their nocturnal activity on moonlit nights by 29.5% and 25.5% respectively, when their diurnal adapted vision is most effective, with approximately half of this activity occurring during peak lion and hyaena activity. In contrast, the larger lion and hyaena showed no change in activity pattern across the lunar cycle (Cozzi et al., 2012). In South America, four felids were examined for temporal niche segregation by Lucherini et al. (2009). There was a large degree of segregation with pampas cat (*Leopradus colocolo*) and Andean cat (*Leopardus jacobita*) showing clear segregation due to shared position as mesopredators whereas both Andean cat and culpeos (*Lycalopex culpeas*) showed significant overlap with puma. However, this is explained on the basis of trophic segregation with puma targeting larger prey when compared to the culpeos and Andean cat which are both mesopredators targeting small to medium sized prey. All four species had activity profiles that were positively skewed toward night time but none of them were influenced by moonlight as the majority of photos occurred during 0% lunar illumination followed by 75 to 100% lunar illumination (Lucherini et al., 2009). Giving up density experiments (GUD) have also been used within the predator guild to examine intraguild competition (Mukherjee et al., 2009). GUDs were conducted on both captive and wild red foxes (*Vulpes vulpes*) in Israel (where the red fox is a mesopredator coexisting with two larger carnivores) the stripped hyaena (*Hyaena hyaena*) and wolf (*Canis lupus pallipes*). The red fox showed a significant increase in activity during the full moon phase of the lunar cycle. This correlated with a decrease in activity of its main predator, the stripped hyaena (Mukherjee et al., 2009).

As a diurnal species, with a visual system optimised for daylight (Peichl, 2005; Roberts, 1951; Sale, 1960), it is hypothesised that if hyrax do indeed show nocturnal activity in the wild that they will show an increase in that nocturnal activity during the full moon phase of the lunar cycle.

Hypothesis:
H_0: There will be no change in the levels of nocturnal activity throughout the lunar cycle.

H_1: If hyraxes show nocturnal activity there will be greater levels of activity during the full moon phase when compared to the new moon phase of the lunar cycle due to the increased light levels afforded by the full moon when compared to the absence of moonlight during the new moon phase.

Predation

For many prey species there is potential to be active outside their known activity pattern; however, it is frequently hypothesised that the activity pattern of their predators restricts their ability to alter their current pattern (Halle, 2000). Sih (1987) explores the importance of refuges and their stabilising effect on predator prey interactions. This balance is achieved when the proportion of prey in refuges decreases with increasing prey density or the proportion of prey in refuges increases with increasing predator density and therefore predation pressure.

Small mammals and the mesopredators within the Iberian Peninsula were examined for their temporal overlap by Monterroso et al. (2013) with surprising results. Two species of murids, (*Apodemus* spp. and *Mus* spp.) show a consistent nocturnal diel cycle despite predation risk from the mesopredators, a group of animals consisting of the red fox, European wild cat (*Felis silvestris silvestris*), stone marten (*Martes foina*), pine marten (*Martes martes*), marten spp. (*Martes* spp.), Eurasian badger (*Meles meles*), common genet (*Genetta genetta*) and Egyptian mongoose (*Herpestes ichneumon*) recorded at two to five times higher at night. In contrast, the only Lagomorph in the study (European rabbit (*Oryctolagus cuniculus*)) showed a crepuscular bimodal diel cycle. The rodent guild appeared to be unaffected by environmental stressors, such as lunar cycle, and European rabbits appeared to be able to suppress the biological tendency for nocturnality in response to increased predation pressure at that time. The mesopredator population was shown to track the rodent activity profile which would deliver a lower energetic input than the rabbits. Accordingly, it is hypothesised that this system evolved for the overall benefit to prey population survival and control but exposes prey at an adequate level for the predator species to prevent them from tracking prey species activity completely.

Another example of the ecological balancing act achieved by predators and their prey was demonstrated by Razo et al. (2010) who presented the activity patterns of coyotes (*Canis latrans*) and their primary prey, two species of lagomorphs (*Lepus californicus, Sylvilagus audobonii*). There was significant symmetry in the evening peak of activity from all three species however the early morning peak for the two prey species was considerably earlier than the coyote. Eriksen et al. (2011) confirmed a similar pattern occurring between wolves (*Canis lupus*) and their main prey, moose (*Alces alces*) in North American where the height of activity from moose occurred at dusk, in opposition to their main predator, the wolf, which showed peak activity levels at dawn.

Non-lethal effects of predation have an equal, if not greater, influence on prey species behaviour than lethal effects (Lima, 1998a). Large mammalian predators have low kill rates when compared to the time invested in hunting (Laundré et al., 2001). This pressure can result in specific adaptations by prey species (Cresswell and Quinn, 2013; Verdolin, 2006). Severud et al. (2011) examined the

effect of wolf (*Canis lupis*) urine on the use of foraging trails by the American beaver (*Castor canadensis*) by monitoring foraging trails using camera traps and found a 95% reduction in the trail visitation rate when wolf urine was applied. This showed that beavers react strongly to olfactory cues of predator presence and demonstrated an extreme example of the non-lethal effect of predation. An efficient way of investigating these effects of predator activity on prey activity patterns is to use camera traps (Kucera and Barrett, 2011).

The two main mammalian predators of hyrax in the Soutpansberg Mountains, the African leopard (*Panthera pardus pardus*) and the brown hyaena, are both known to predate upon one or both species of hyrax (Norton and Henley, 1987; Skinner and Van Aarde, 1981), particularly leopards for which hyrax have been estimated to account for 20% of prey consumed in the area (Chase-Grey, 2011a). Hyraxes are also under threat from avian predators albeit limited to daylight hours. The Verreaux's or black eagle and crowned eagle are the two most common avian predators of hyrax (Barry and Barry, 1996; Boshoff et al., 1994; Davies, 1994). However, their hunting ability is restricted by weather conditions as they require adequate temperatures during daylight hours to enable the formation of thermals within the atmosphere to maintain flight (Loon, 2005; Olsen et al., 2006). The typical activity patterns of these two groups of predators means that they are active at different times within the 24-hour period with a minimal potential for overlap.

It could be that the low levels of deep sleep in rock and bush hyrax reported above could be part of an anti-predation mechanism. Retaining some level of vigilance for as much of the diel cycle as possible but satisfying physiological requirements for rest (Lesku et al., 2006). Therefore, it is hypothesised that predation could be a constraining factor on the potential for hyrax to utilise the dark hours of the 24-hour cycle and show increased nocturnality.

Hypothesis:
H_0: The presence of predators had no impact on the activity pattern of hyrax across the 24-hour period.

H_1: The presence of predators had a negative impact on the ability of hyrax to utilise the dark hours of the 24-hour period and restricted their nocturnality.

Using the interactions between hyrax physiology and its environment the sleep-wake cycle of two species of hyrax was examined using camera trap images to determine the effects of day length, lunar cycle and predation.

Methodology

Study site

The study was conducted at the Lajuma Research Centre located in northern South Africa within the western Soutpansberg Mountains, Limpopo Province, South Africa (23°02'17.1"S 29°26'26.5"E) (see Chapter 2: Figure 2.5). The site is part of the Vhembe Biosphere, designated in 2009 (Pool-Stanvliet, 2013), and is a biodiversity hotspot which supports healthy populations of both large mammalian carnivores and raptors among other species (Grey et al., 2013). This diversity is maintained by varied flora and climate.

Data collection

The Primate and Predator Project (PPP), based at Lajuma Research Centre has been conducting camera trapping in the area since 2011 producing data on activity patterns of both mammalian predators and their prey from across the Soutpansberg Mountains. Further to the PPP cameras, an additional array of cameras was set up in a separate area to capture hyrax activity. All cameras used for this study were either Reconyx Hyperfire H500 or Reconyx Hyperfire H600. For a detailed description of camera placement for this study see Chapter 2: Camera trapping.

This study examined two species of hyrax, rock hyrax and bush hyrax, which both inhabit the study site and in several locations, live sympatrically. Due to the chosen method of data collection, it was difficult to identify animals to species level in some camera trap images. Furthermore, due to the presence of sympatric colonies within the study site and previous literature detailing similarities in behaviour, especially at colonies, the decision was made to group the two species in order to maximise data. Herein, the two species are grouped and referred to as hyrax.

The total number of images of hyrax captured by the two camera arrays was 10,367 (Table 3.1 for image totals of individual camera arrays); however only the PPP cameras captured predators with a total of 81,585 being included in this category comprising 11 different species (leopard, caracal, honey badger (*Mellivora capensis*), African wildcat (*Felis silvestris lybica*), serval (*Leptailurus serval*), African wild dog (*Lycaon pictus*), brown hyaena, civet (*Civettictis civetta*), large spotted genet (*Genetta tigrina*), spotted hyaena and black backed jackal).

Table 3.1: Number of images collected from the two camera trapping methods.

Hyrax cameras		Primate and Predator Project cameras		Total
Images of hyrax	6174	Images of hyrax	4193	10,367
Images of predators	0	Images of predators	81585	81585

Data analysis

To explore the temporal activity patterns of hyrax, camera trap photographs were filtered to include only independent photographs, where the image captures a behavioural event that is independent of the behavioural event captured in the previous image (LaFleur et al., 2014; van Schaik and Griffiths, 1996). The methodology of classifying independent images from camera trapping varies within the literature and is related to habitat and focal species. LaFleur et al. (2014) used camera traps to monitor night time movement of ring tailed lemurs in Madagascar and chose a 1 hour interval of independence as previous behavioural observations had shown that the lemurs left and returned to the sleeping site within an hour and this was classed as a singular behavioural event. Silver (2004) used two types of camera, both using 35 mm film, to study jaguar (*Panthera onca*) in Belize and Bolivia. The cameras had different detection methods, one used infrared beam and the other a heat and motion sensor. They employed the CAPTURE software package to catalogue and analyse the images therefore they do not state the classification of independence for their images. Tobler et al. (2008) followed the methodology in Silver (2004) again to study jaguars however they chose a 1 hour time interval for independent images giving size of study species and home range as the justification for the chosen interval. However, a study conducted in the Brazilian rainforest selected images that were more than 5 minutes apart as they were sampling a wide range of species and a shorter interval between images is better for capturing smaller species. When using motion sensor cameras, as is the case in this study, Hamel et al. (2013) suggest an interval of 20 minutes between images. They justify this recommendation as a way of balancing the raw error rate (number of unusable images/number of successful images) and the amount of time required to process the images. Here an interval of 15 minutes was chosen to define independent photographs of the same species at the same site.

The predator data set was constructed in a similar way to the hyrax dataset. Images that were separated by 15 minutes or more were compiled and then, using an ExifTool (Harvey, 2016), the metadata (time, temperature, lunar phase etc.) was extracted from the images. The site/camera, species, time which is transformed into decimal format between zero and one (0.00 = 00:00 - 0.99... = 23:59) and lunar phase were collated in a comma separated file (.csv) for analysis in R (R Core Team, 2014). This same procedure was carried out for the hyrax images (see Chapter 2).

The method employed with the Overlap package views the data as a random sample from an underlying distribution that describes the probability of a photograph being taken during any particular time of day. In this case the independent images of hyrax or their predators being analysed are a random sample of their behaviour across the 24-hour period. The probability density function of this distribution is then referred to as the activity pattern, which assumes that the animal, in this case a hyrax or one of its predators, is equally likely to be photographed at all times when it is active (Ridout and Linkie, 2009). Overlap works by quantifying the level of overlap between two activity patterns, for example hyrax activity patterns and leopard activity patterns, allowing the interaction between the two to be assessed. Initially, the activity pattern for both hyrax and leopard was estimated separately, non-parametrically, using kernel density estimation (Schmid and Schmidt, 2006). Next, a measure of overlap between the two estimated distributions was calculated. There are a number of methods that can be used for this process, as reviewed by Ridout and Linkie (2009). The coefficient of overlapping (D) is used here and produces a result that ranges from 0 (no overlap) to 1 (complete overlap) (Weitzman, 1970). This is defined as the area under the curve that is formed by the smaller of the two density functions at each time point. One useful interpretation of the coefficient of overlapping is that for any time period during the day, the probability that a randomly selected camera trap photograph will have occurred during that period differs between the two distributions by 1–D. Ridout and Linkie (2009) presented three alternative ways of estimating D, given estimates of the two probability density functions: Dhat1 (Δ_1), Dhat4 (Δ_4) and Dhat5 (Δ_5) as described in (Schmid and Schmidt, 2006). Ridout and Linkie (2009) suggest that for analysis where the smaller sample size is >75 Dhat4 (Δ_4) is used however for analysis where the smallest sample size is <75, Dhat1 (Δ_1) is more appropriate. This differs to the recommendation by Schmid and Schmidt (2006) who recommend Dhat5 (Δ_5) for smaller sample sizes but Ridout and Linkie (2009) show Dhat1 (Δ_1) is more accurate for the highly variable data likely to be collected in the field.

The variable of lunar phase was initially extracted from the camera trap images and fell into one of four categories: full moon, waxing gibbous, first quarter, old crescent, new moon, new crescent, last quarter and waning gibbous. It was then further modified into three categories: new moon, full moon and partial moon which consisted of waxing and waning gibbous, first and last quarter and old and new crescent moon phases. These new categories were then applied to the corresponding data points for analysis.

Hours of twilight were determined by the average sunrise and sunset across the year (approximately 06:00 for sunrise and 18:00 for sunset) allowing for an hour of twilight either side following the protocol used in Ridout and Linkie (2009). Day length was based on season with summer having the longest days (most hours of daylight) and winter having the shortest days (least

hours of daylight) with sunrise and sunset calculated via Geoscience Australia (2015a) web based calculator using the geographical coordinates of Lajuma Research Centre. The definition of sunrise and sunset used by this calculator is the instant in the morning or evening under ideal meteorological conditions, with standard refraction of the sun's rays, when the upper edge of the sun's disk is coincident with an ideal horizon (Geoscience Australia, 2015b).

Four variables (time, species, lunar cycle and day length) were analysed using the 'Overlap' package (Meredith and Ridout, 2014). 'Overlap' requires the time variable to be in radians, this transformation was done within the package (Meredith and Ridout, 2014). Time in radians is a circular format which allows for activity to be plotted continuously across the 24-hour period. In the absence of data points, overlap uses kernel density estimation and a smoothing factor (average set to kmax = 3) to estimate the density of activity at any given time. Estimate of overlap Dhat4 (Δ_4) was chosen as the appropriate estimate according to sample size categories specified by Ridout and Linkie (2011) with one exception being spotted hyaena for which Dhat1 (Δ_1) was chosen due to the low sample size.

Statistical analysis

The density of activity at 15 minute intervals for hyrax and their mammalian predators was extracted by creating an object containing the densities from the 'densityPlot' function within the Overlap package (Ridout, 2014). These data were then exported as a data frame. Density of activity for hyrax and their predators was then explored using non-linear regression in R (R Core Team, 2014). A Shapiro-Wilk test was conducted on both the hyrax and predator datasets to establish the presence of normality. Once the absence of normality was confirmed, a non-parametric test, Mann-Whitney U test, which is a test of differences, was performed on lunar phase and day length datasets for hyrax and predators combined. When examining individual relationships between density of activity of predatory species and density of activity of hyrax the non-parametric Spearman's rank test was used to quantify the relationship.

Results

The sleep-wake cycle of hyrax in the Soutpansberg Mountains was predominantly diurnal: 91.6% of activity occurred during the hours of 05:00 and 19:00 with activity peaking in the late afternoon, climaxing at 18:00 (Figure 3.1 (top)). However, there was a low but consistent level of nocturnal activity detected between the hours of 19:00 and 05:00 throughout the study area (8.4% of total activity; Figure 3.1 (bottom)) suggesting that certain factors may allow for nocturnal activity. Both plots within Figure 3.1 use an identical data set but the x axis has been centred on midday (top) and midnight (bottom) to better visualise the diurnal and nocturnal activity profiles, this is in line with previous publications of Overlap analysis.
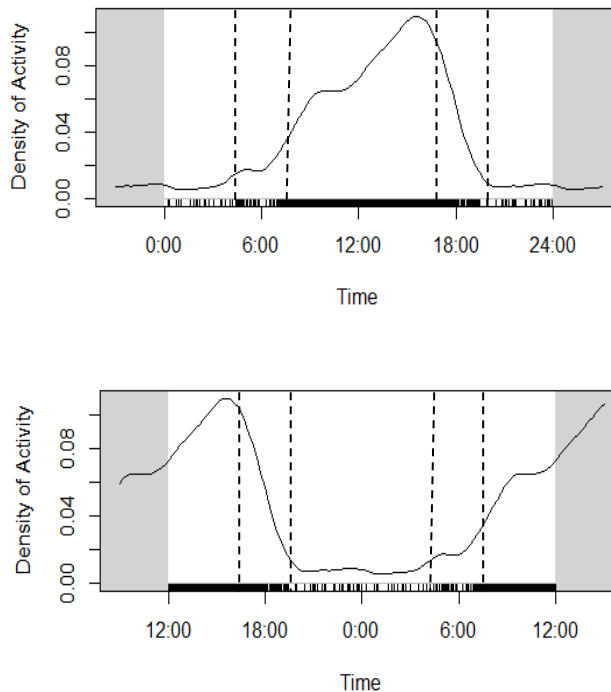
Figure 3.1: Diurnal (top) and nocturnal (bottom) activity profile for two species of hyrax in the Soutpansberg Mountains, South Africa. The broken lines indicate the shift in the time of sunrise and sunset (dawn and dusk) throughout the year and the grey sections indicate that the data is continuous on a 24-hour cycle. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed. These plots have been constructed using identical data however the x axis has been centred on midday (top) and midnight (bottom) to emphasise the two separate activity patterns.

Day length
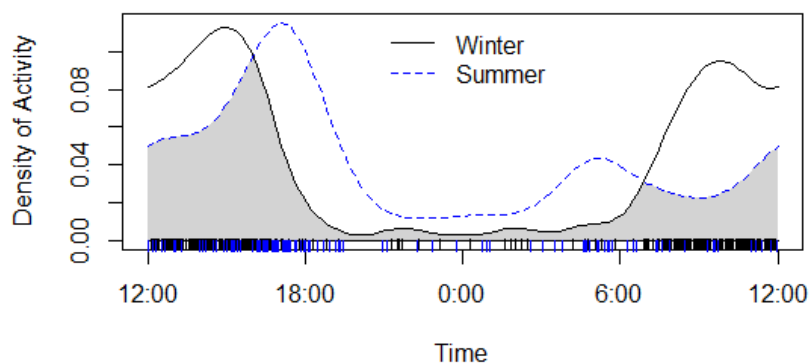
Figure 3.2: Nocturnal activity levels of hyrax within the Soutpansberg Mountains throughout the winter season (shortest days/longest night) and summer season (longest days/shortest nights); estimation of overlap $\Delta_4 = 0.60$. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Due to the rejection of the hypothesis of normality from the Shapiro-Wilk test for normality (Table 3.2), the non-parametric Mann-Whitney U test of differences was used to test the difference in density of activity during the nocturnal phase of summer and winter. The data were restricted to the dark hours of the 24-hour cycle by using only data collected between the hours of 19:00 and 05:00 in summer and 17:00 and 07:00 in winter. Contrary to predictions, a significant increase in nocturnal activity was evident during the summer months (Figure 3.2; n = 41; V = 861; p = < 0.001).

Table 3.2: Statistical tests of 24-hour density of activity and nocturnal density of activity data for hyrax comparing activity across summer and winter evaluating the effect of day length on level of nocturnal activity.

NOCTURNAL ACTIVITY			
Shapiro-Wilk Normality Test	**n**	**W**	**P**
Summer	41	0.78	< 0.001
Winter		0.94	0.041
Mann-Whitney U Test	**n**	**V**	**P**
Summer and Winter	41	861	< 0.001

Lunar cycle

The estimated overlap between hyrax density of activity during the new moon and full moon phases was 89% across the 24-hour period. Subtle differences exist in the pattern of overlap of density of activity of hyrax between new and full moon phases (Figure 3.3) with an apparent increase in activity in the middle of the new moon lunar phase compared to the full moon lunar phase.
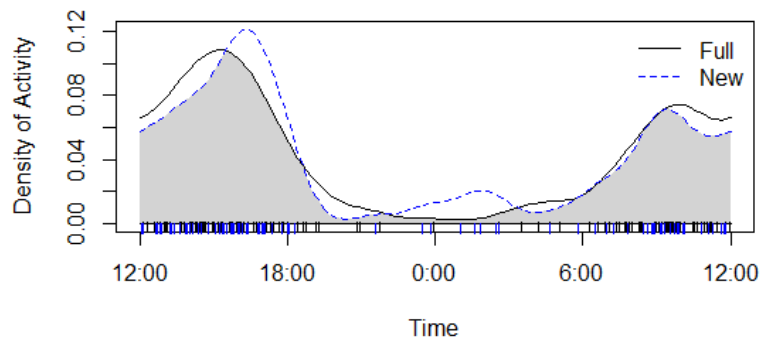
Figure 3.3: Overlap analysis for nocturnal activity of hyrax showing full moon and new moon lunar phases. Estimation of overlap for hyrax is Δ_4 = 0.886. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

The estimated overlap between mammalian predators (species included: leopard, caracal, honey badger, African wildcat, serval, African wild dog, brown hyaena, civet, large spotted genet, spotted hyaena and black backed jackal) density of activity during the new moon and full moon phases was 89% across the 24-hour period, identical to the level of overlap between these lunar phases recorded for hyrax. Though, as with the hyrax density of activity, there was a difference in the pattern of overlap of density of activity of mammalian predators between the two moon phases (Figure 3.4). The density of activity of mammalian predators across the new moon lunar phase remained fairly consistent with small peaks across the dark hours. However, an apparent increase in activity at the beginning of the nocturnal phase during the full moon lunar phase was detected for the mammalian predator population.
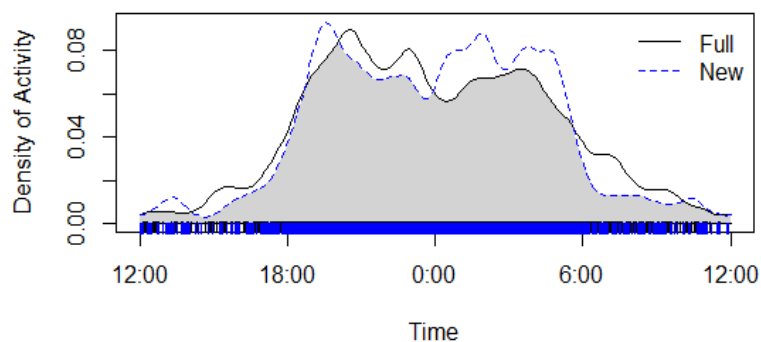
Figure 3.4: Overlap analysis for nocturnal activity of a selection of mammalian predators (leopard, caracal, honey badger, African wildcat, serval, African wild dog, brown hyaena, civet, large spotted genet, spotted hyaena and black backed jackal) showing full moon and new moon lunar phases. Estimation of overlap for mammalian predators is Δ_4 = 0.892. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Three out of four densities obtained from the overlap analysis of lunar phase activity in Figure 3.3 and Figure 3.4 were not normally distributed (Table 3.3). The analysis was restricted to between 19:00 and 05:00 to ensure only hours of darkness across the whole year were considered. There was no significant difference between density of activity of the predator guild between the new

and full moon lunar phases (Mann-Whitney U test: n = 41; V = 558; p = 0.10). Therefore, it can be concluded that the variation in density of activity of predators across full and new moon lunar phases was not significant, eliminating predator activity across moon phases as the causal effect on variations in hyrax activity across lunar phases (Table 3.3).

The above analysis was replicated for hyrax density of activity and limited to the nocturnal period for new and full moon lunar phases and, like the predators, the difference between activity during the new moon lunar phase and the full moon lunar phase was not significant (Mann-Whitney U test: n = 41; V = 528; p = 0.21). This demonstrates that lunar phase had no impact on the nocturnal activity of hyrax.

Table 3.3: Summary of statistical analysis of density of activity of hyrax and their mammalian predators during the complete 24-hour period and the dark hours of the 24-hour period (nocturnal activity only) comparing the new and full moon lunar phases. *Non-significant relationship = data is normally distributed.

NOCTURNAL ACTIVITY				
Shapiro-Wilk Normality Test				
Group	Lunar phase	n	W	P
Hyrax	New	41	0.70	< 0.001
	Full	41	0.78	< 0.001
Predators	New	41	0.87	< 0.001
	Full	41	0.96	0.15*
Mann-Whitney U Test				
Group	n	V	p	
Hyrax	41	528	0.21	
Predators	41	558	0.10	

Predator activity

Figure 3.5 shows the combined activity patterns of the main mammalian predators in the Soutpansberg Mountains overlapped with hyrax activity demonstrating a strong nocturnal behavioural pattern for the mammalian predators. The estimation of overlap (Dhat4 Δ_4) produced from this analysis shows that the overlap of activity between the predators and the hyrax is 29% across the 24-hour period suggesting that hyraxes are successful in avoiding periods of greatest collective predation risk. Further examination of the density of activity for hyrax and their predators using a Spearman's rank test revealed a strong negative correlation (ρ = -0.86; n = 96; p<0.001).

However, when individual species from within the predator guild are overlapped with hyrax activity, significant differences in overlap exist between predators and hyrax (Table 3.4).

Table 3.4: Some of the mammalian predator species captured on camera traps in the Soutpansberg Mountains and their percentage overlap of activity with hyrax across the 24-hour period; *Dhat1 (Δ_1) overlap estimate was chosen for Spotted hyaena due to small sample size (<75).

Species	Percentage of overlap with hyrax activity across the 24 hours
Leopard	45%
Caracal	42%
Honey badger	36%
African wildcat	33%
Serval	28%
African wild dog	18%
Brown hyaena	17%
Civet	16%
Spotted hyaena*	16%
Large spotted genet	15%
Black backed jackal	10%
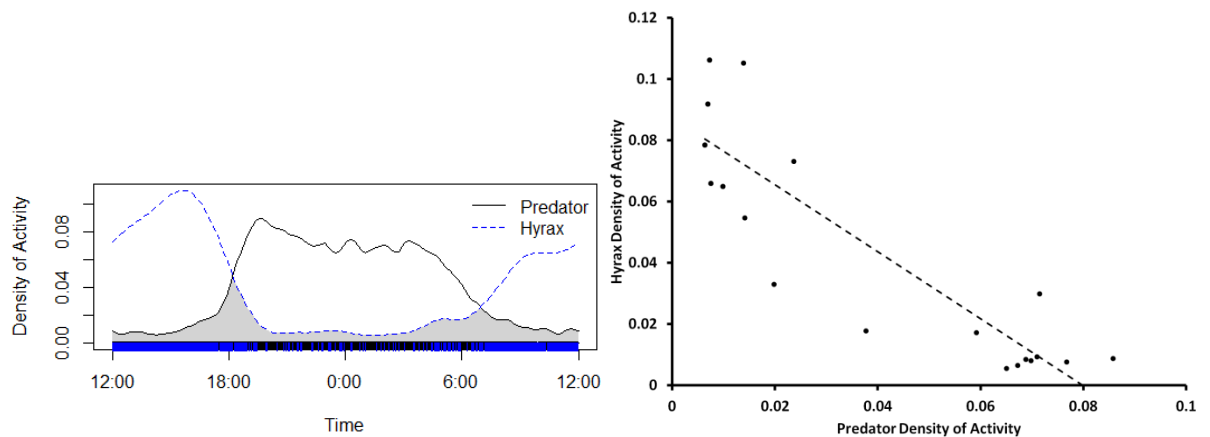
Figure 3.5: Nocturnal activity of a portion of the mammalian predators in the Soutpansberg Mountains overlaped with nocturnal activity of two species of hyrax from the same region (left); estimation of overlap Δ_4 = 0.29 (left). Hourly density of activity of hyrax and their mammalian predators over the 24 hour period with a line of best fit for visual interpretation only (right). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Figure 3.6 through to Figure 3.8 examine the overlap of density of activity of leopard, caracal and brown hyaena respectively with hyrax density of activity and present a breakdown of the activity profiles of the main mammalian predators and their possible impact on hyrax density of activity.
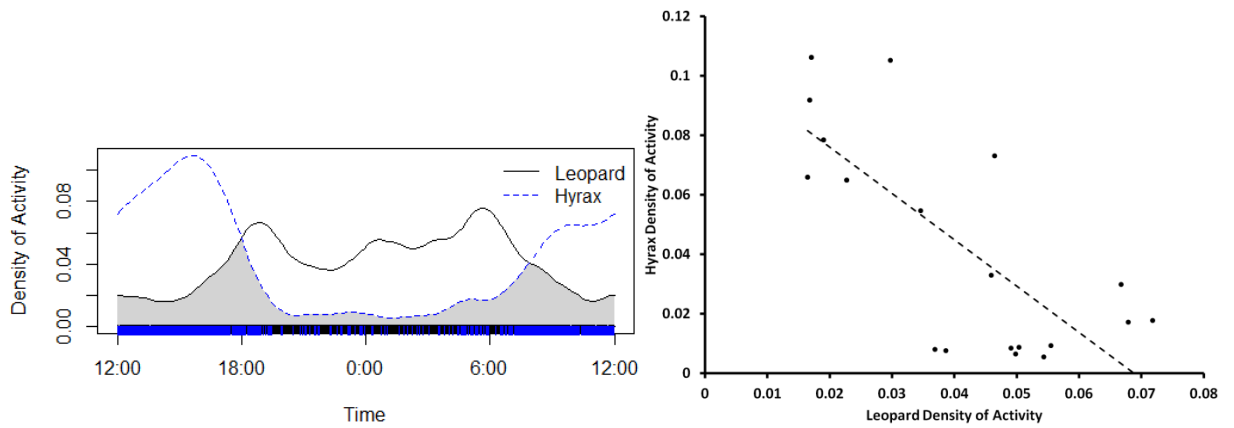
Figure 3.6: Nocturnal activity patterns for a proportion of the leopard population in the Soutpansberg Mountains overlapped with hyrax activity from the same area; estimation of overlap Δ₄ = 0.446 (left). Hourly density of activity of hyrax and leopard over the 24-hour period with a line of best fit for visual interpretation only (right). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Leopards and hyrax are shown to be active simultaneously 45% of the time across the 24-hour period. A Spearman's rank test was conducted on the leopard and hyrax density outputs resulting in a negative correlation (Figure 3.6; ρ = -0.73; n = 96; p < 0.001).
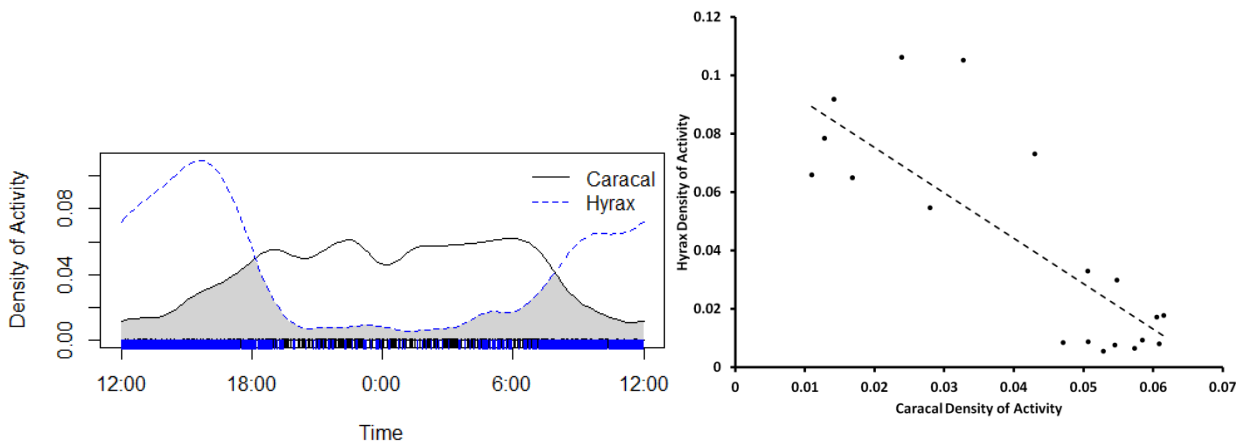
Figure 3.7: Nocturnal activity patterns of a proportion of the caracal and hyrax populations in the Soutpansberg Mountains; estimation of overlap Δ₄ = 0.418 (left). Hourly density of activity of hyrax and caracal over the 24-hour period with a line of best fit for visual interpretation only (right). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Caracals show a comparable level of activity overlap with hyrax to leopards with a reading of 42% overlap across the 24 hour period. When caracal and hyrax densties are plotted the Spearman's rank correlation (Figure 3.7; ρ = -0.72; n = 96; p < 0.001) it shows a strong negative realtionship between the activity patterns of the two species.
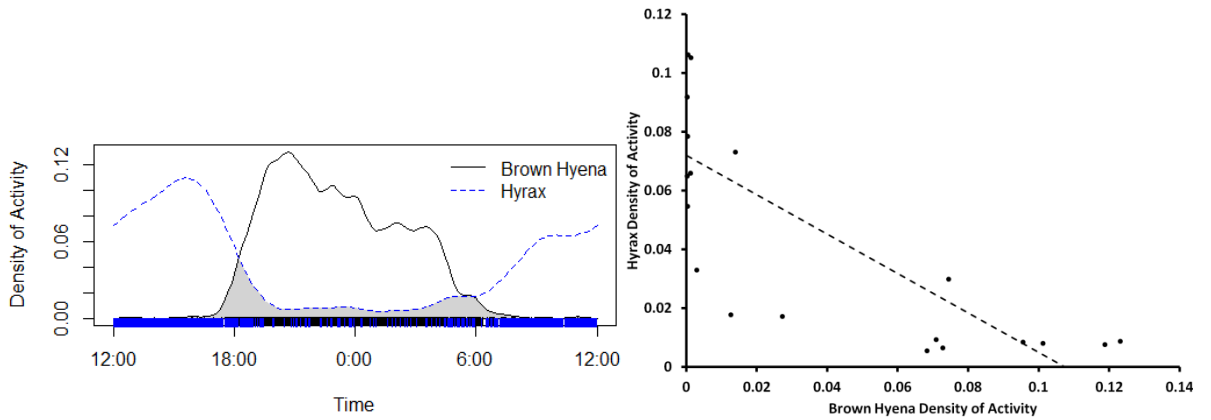
Figure 3.8: Nocturnal activity patterns of a proportion of the brown hyaena and hyrax populations in the Soutpansberg Mountains; estimation of overlap Δ_4 = 0.166 (left). Hourly densities of hyrax and brown hyaena over the 24-hour period with a line of best fit for visual interpretation only (right). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

In contrast to both leopards and caracals, the estimated overlap of activity between brown hyaena and hyrax is 17%. As with leopard and caracal, a Spearman's rank test was conducted on the density output of brown hyaena and hyrax, resulting in a negative correlation (Figure 3.8; ρ = -0.80; n = 96; $p < 0.001$), which is a strong negative correlation between the densities of the two species throughout the 24-hour period.

Discussion

Activity patterns can be a useful tool when exploring an animals' interaction with environmental variables such as day length, lunar cycle and predation pressure (Halle, 2000). In this study a camera trapping protocol was exercised to investigate the activity patterns of two species of hyrax and a number of their mammalian predators.

Nocturnal activity accounted for 8.4% of total density of activity recorded for both species of hyrax in the Soutpansberg Mountains; with the level of nocturnal activity largely influenced by predation pressure. Similar findings have been reported in the diurnal ring tailed lemur by Donati et al. (2013) who showed that in some parts of its range up to 12.81% (± 1.94%) of activity was during the hours of darkness. The diurnal Verreaux's sifaka (*Propithecus v. verreauxi*), another lemur species, was monitored using accelerometers by Ekert and Kappeler (2004) which showed 10% of activity detected occurred during the rest period (hours of darkness) but due to the sensitivity of the device this was most likely subtle movements that occurred whilst the animal was sleeping which was supported by opportunistic behavioural observations. The authors noted however that short movements due to disturbance by predators or conspecifics could not be eliminated as a cause. Halle (2006) uses both shrews and voles as examples of small mammals that use cathemerality to overcome energy and dietary needs respectively, specifically showing that shrews are cathemeral due to a need to feed throughout the 24-hour period. The variability in other diurnal and cathemeral mammals' nocturnal activity gives some indication of the spectrum of cathemerality and its causation within mammals.

The evidence of nocturnal activity within a strong diurnal pattern demonstrated by hyrax in the Soutpansberg Mountains does go some way to supporting the polycyclic sleep-wake pattern shown to occur in hyrax in a laboratory setting by Gravett (2012). With hyrax being reported as having unusually low levels of REM sleep (Allison and Cicchetti, 1976) and this trait being linked with high levels of predation by Lesku et al. (2006) it is not unexpected to observe hyrax being active during the dark hours. How consistent this activity is across their range is unknown as the majority of behavioural studies done on rock and bush hyrax to date have been primarily focused on daytime activities such as foraging (Coe, 1962; Druce et al., 2006; Fourie and Perrin, 1989; Kotler et al., 1999; Sale, 1965a; Sale, 1966a), social structure (Barocas et al., 2011; Barry and Mundy, 1998; Barry and Mundy, 2002; Brown and Downs, 2005; Canady, 2012; Koren and Geffen, 2009; Koren et al., 2008), thermoregulation (Brown and Downs, 2005, 2006; Brown and Downs, 2007; Meltzer, 1973; Sale, 1970; Taylor and Sale, 1969) and reproduction (Barry and Mundy, 1998; Barry, 1994; Barry et al., 2014; Barry and Mundy, 2002; Demartsev et al., 2014; Fourie, 1984; Glover and Sale, 1968; Hanks, 1977; Mendelssohn, 1965; Sale, 1965b). To fully understand the 24-hour sleep-wake cycle of rock

and bush hyrax more comprehensive studies using non-invasive methods such as camera traps are required to collect reliable data on nocturnal activity across their entire range.

Day length

The time restrictions placed on an animal that is strictly diurnal in winter, where days are shorter, can alter the order and duration of tasks the animal completes (Hill et al., 2003). In the case of hyrax in the Soutpansberg Mountains it was hypothesised that these diurnal animals may show a higher level of nocturnal activity during the winter months when daylight hours are significantly reduced. This hypothesis is rejected because there was a significantly higher level of activity detected during the summer months compared to the winter months. A possible explanation could be linked with the hyraxes' inability to adequately control their internal body temperature (Sale, 1970; Taylor and Sale, 1969). During the summer season daytime temperatures may exceed tolerable levels preventing hyrax from foraging during daylight hours (Brown and Downs, 2006; Downs et al., 2013; Sale, 1970; Taylor and Sale, 1969). However, utilising the consistently higher twilight and night time temperatures of the summer months may enable hyrax to compensate by foraging in the twilight and dark hours. Conversely, the twilight and evening period may be inaccessible for hyrax due to the average temperatures falling below the thermoneutral zone of hyrax (Brown and Downs, 2005; Meltzer, 1973; Sale, 1970).

Lunar cycle

There were no significant differences in activity between the new and full moon lunar phases suggesting that the lunar cycle has little impact on nocturnal activity in hyraxes. This result is surprising given that hyrax showed potential for nocturnal activity when observed in a laboratory environment and have the visual system to enable adequate vision on moonlit nights (Gravett et al., 2012; Peichl, 2005). Furthermore, the lunar phase has been documented to have an effect across the animal kingdom and on a variety of behavioural process including primate activity profiles (Kappeler and Erkert, 2003), seal foraging behaviour and anti-predation behaviour of their prey (Horning and Trillmich, 1999) as well as on amphibian copulation (Grant et al., 2009). It is clear that the predator activity remains consistently high across the lunar cycle, which may be a strong force acting on hyrax and preventing them from utilising this part of the 24-hour period on moonlit nights.

The association of increased predation risk with increased lunar illumination is well established in other species (Kotler et al., 2010; Mougeot and Bretagnolle, 2000; Schmitz, 1998). However, a

meta-analysis conducted by Prugh and Golden (2014) points to a shortage of literature on the ability of prey species to detect predators and the increase in foraging efficiency that may be afforded them on moonlit nights. The meta-analysis was conducted on 59 nocturnal mammal species and tested the assumption that moonlight increased predation risk and took into account trophic level, habitat cover and visual acuity. Moonlit nights decreased activity across all species but in prey species this effect was better explained by phylogenetic relatedness, visual acuity and habitat cover and not trophic level as is often hypothesised. Activity during moonlit nights was highest in visually orientated species, lowest in open habitat types and showed a taxonomic trend with primates showing higher levels of activity on moonlit nights when compared to rodents, lagomorphs, bats and carnivores. Prugh and Golden (2014) conclude that habitat cover and visual acuity combine to moderate the effect of moonlight but trophic level has a minimal effect and that, despite the net effect of moonlight being an increase in predation risk, caution should be taken when assessing this effect by considering other factors such as sensory systems and phylogenetic history. In the context of the meta-analysis by Prugh and Golden (2014) a more comprehensive study of nocturnal activity by hyrax across the lunar cycle may contribute to a better understanding of the effect of moonlight on the nocturnal activity profile of hyrax, a species that is heavily predated upon.

Predation

Although hyrax show consistent, low levels of nocturnal activity, increases in nocturnal behaviour do not appear to follow the predictions of hyrax using the nocturnal period flexibly when conditions are favourable. This suggests that there may be significant constraints on using the nocturnal environment. The combined mammalian predator overlap estimate emphasises a non-lethal effect of predation by showing the times at which possible mammalian predators of hyrax are active and when this threat is at its most severe. Although not all the predators included in this group are known to prey on hyrax in the area they are grouped within the same guilds as known predators of hyrax and could therefore still be detected as a threat due to giving similar indirect olfactory and auditory cues as known predators. An example of this is the similar behaviour profile of caracals and leopards. It is unknown whether caracals in the Soutpansberg Mountains prey on hyrax however they have been documented to prey on hyrax in other parts of their range (Avenant and Nel, 2002; Barry and Mundy, 2002; Palmer and Fairall, 1988; Stuart and Stuart, 1993) and therefore, could have a similarly constant threat level for hyrax living in the area. Although they are classed as a mesopredator and may not present the equivalent threat to hyrax as leopards do. This could be the focus of further study by investigating the composition of the diet of caracals within the

Soutpansberg Mountains in order to quantify their impact on the hyrax population and therefore infer their effect on hyrax activity patterns.

Another predator whose impact on hyrax within the Soutpansberg Mountains in unquantified is the brown hyaena. This study has shown them to be a definitive nocturnal species and there is preliminary evidence that brown hyaena present within the Soutpansberg Mountains may prey on the two hyrax species (Williams, K. Pers. comm. 2015) as they have been shown to do in the past in other parts of Africa (Cruz-Uribe, 1991; Klein and Cruz-Uribe, 1996). Accordingly, it is possible that the brown hyaena is exerting the most predation pressure across the nocturnal period on the hyrax population. However, there is likely to be a stronger cumulative effect of predation because when mammalian predators were grouped together and overlapped with hyrax density of activity they had a stronger negative effect than individual predator density of activity.

An understudied element of non-lethal effects of predation is the cumulative effect that multiple predators could be exerting on prey species. However, the effect that the presence and absence of predators can have on prey behaviour is known. For example, Tambling et al. (2015) showed that large prey species within the Addo National park, South Africa shifted their diel cycle towards nocturnality in the absence of predators but when predators were reintroduced the prey species reverted to a diurnal activity profile. The Soutpansberg Mountains could be a good location for examining the cumulative effect that predators, both mammalian and avian have on prey species as it sustains a diverse group of predators that, due to competition, are likely to naturally occur at different densities across the mountain range creating natural gradients for such a study (Berger et al., 2003; Chase-Grey, 2011a; Fitzgerald, 2015b; Schwarz and Fischer, 2006; Stuart and Stuart, 1993).

Finally, when considering the impact of non-lethal predation, it should be noted that the avian predator guild is absent from this study as the activity pattern data is currently not available for the black and crowned eagles that are known to inhabit the study site. Their impact on hyrax can be hypothesised from previous studies conducted throughout black and crowned eagle territories which have shown that both raptor species are diurnal, weather dependent hunters (Barry and Barry, 1996; Boshoff et al, 1994; Chiweshe, 2007; Davies, 1994; Gargett, 1977; Jarvis et al., 1980; Symes and Antonites, 2014). There would most likely be a relationship between raptor and hyrax activity since both species of raptor are known to prey on the two species of hyrax in other parts of their range and there is evidence for an evolutionary adaptation in the eye morphology of the diurnal rock hyrax to aid in aerial predator detection (Barry and Barry, 1996; Boshoff et al., 1994; Chiweshe, 2007; Gargett, 1977; Jarvis et al., 1980; Millar, 1973).

Conclusion and Future Directions

There are three main conclusions from this study:

1. The effect of day length on hyrax manifests itself in an increase in nocturnal activity during the summer months. This is in opposition to the hypothesised effect of day length which predicted a higher level of nocturnal activity in winter when days are shorter.

2. Lunar phase was shown to have no impact on nocturnal density of activity for hyrax or their mammalian predators. Therefore, the hypothesis of an increase in nocturnal activity during the full moon lunar phase is rejected. Further supporting evidence for rejecting this hypothesis can be seen in the absence of variation in predator activity between the two lunar phases.

3. The hypothesis of a negative effect of predator density of activity on hyrax density of activity was confirmed. It was also demonstrated that predators have a cumulative negative effect.

The initial finding supports published evidence that hyrax are poor thermoregulators: their inability to control their body temperature when the environmental ambient temperature varies restricts their nocturnal activity in winter but allows them to utilise the dark period of the 24-hour cycle in summer when the overnight temperature remains within their thermoneutral zone. This results in the rejection of the hypothesis that hyrax would extend activity into the dark hours during the winter months as a result of the shorter days and the resultant time constraint on daily activity patterns.

In addition, from this analysis the lunar phase was eliminated as a factor effecting nocturnal activity, which was surprising. An examination of the same relationship in mammalian predators showed no difference. This led to the conclusion that the risk of predation during the nocturnal phase across the lunar cycle was so high that the increase in moonlight during the full moon phase (to aid predator detection by the hyrax) was not adequate to reduce or eliminate the increased risk of foraging at night. Furthermore, the energetic gain of foraging in such dangerous conditions was not substantial enough to facilitate such risky behaviour.

It is acknowledged that this is a very coarse analysis that uses finite boundaries for day and night and for diurnal and nocturnal activity, all without considering the fine scale changes in light levels that undoubtedly occur during the dark hours of the 24-hour period. A future direction for this area of research would be to utilise data on lunar luminosity and the fine scale changes in the lunar cycle

and additional weather parameters such as cloud cover to continue to tease apart nocturnal behaviour in hyrax and their predators and to determine if varying levels of lunar luminosity play a role in the levels of nocturnal activity in hyrax and their predators (Donati and Borgogninia-Tarli, 2006). Additionally, not all ultimate factors affecting activity patterns were examined here. Avoidance of competition and metabolic dietary related demands were absent from this study, of which either or both could have a significant influence on hyraxes' activity patterns and could be explored within the hyrax populations in the Soutpansberg Mountains (Bider, 1968; Donati et al., 2009).

If these findings are robust then predation risk is the driving factor behind the minimal nocturnal activity detected from hyrax in the Soutpansberg Mountains. Therefore, similar questions could be asked of populations that are under a reduced risk of predation or are housed in a predator free environment, such as zoological collections or predator free reserves allowing for comparison. Investigating the sleep-wake cycle of hyraxes that are not under the threat of predation may allow for the isolation of variables that influence the sleep-wake cycle in hyrax.

Chapter 4 : Activity patterns of two species of hyrax in a mountainous environment in relation to weather and fine scale habitat variation

Introduction

Animals have evolved to take advantage of increases in resources and beneficial changes in environmental conditions to increase reproductive success, and in turn overall fitness, by filling various temporal and spatial niches (Nelson et al., 1990). This can manifest itself in behavioural changes that may occur as a direct response to environmental fluctuations. For instance, seasonally breeding animals must identify and react to environmental cues that can signal the start and or the end of seasons that favour reproductive success (Nelson et al., 1990). However the cues used by animals to predict environmental changes may not have direct survival value and can be broken down into two categories: proximate and ultimate (Baker, 1938). Some ultimate factors such as food availability can also be classed as proximate factors, whereas day length and weather variables including temperature and rainfall are definitively proximate (Nelson et al., 1990).

Factors that interfere with advantageous environmental change include weather, inanimate resource availability, such as shelter, and the presence of conspecifics for reproduction (Dingle, 2006; Dingle and Drake, 2007). To satisfy these requirements some animals participate in large scale migration, such as the large ungulate migrations in North America and Africa (Craighead et al., 1972; Fancy et al., 1989; Holdo et al., 2009) and avian migrations between Europe and Africa (Newton, 2003). The key ecological processes used to explain the evolution of migration in birds are of food limitation, predation, and intolerance of climatic conditions (Boyle, 2006). These factors also affect other animal groups, including small mammals which only show small scale shifts in patterns of activity across their range but these can be just as informative about their behavioural ecology (Kotler et al., 1999).

Temperature and rainfall, in certain situations, can both be proximate ecological drivers of behaviour. In this study, I examine the impact of temperature and rainfall on the activity profile of hyraxes in northern South Africa that show clearly defined variability in their behaviour. This variability may be a product of satisfying the species requirements for food, rest and social interaction. Both temperature (seasonal variance) and habitat (or site specific variation) will be examined for the extent to which they influence these behaviours and the activity profile in general (Barry and Shoshani, 2000; Olds and Shoshani, 1982).

Effect of weather variation on activity

Many animals have evolved ways of coping with changes in weather conditions throughout the seasons, such as birds migrating to avoid harsh winters (Berthold, 2001). American and European bear species avoid the winter by hibernating, preparing their bodies during the summer and then using these stored resources to allow them to sleep for months at a time (Watts et al., 1981). These examples are at the extreme end of the scale; however, there are animals that either do not need to or do not have the physical capability to migrate or hibernate. For oceanic seabirds residing in tropical equatorial waters, there is no seasonal effect and biological events, such as moulting and breeding, are only limited by the physiological constraints of their body. Whereas animals either side of the equator can either alter their 24 hour sleep wake cycle or modify how much time they dedicate to certain activities in response to environmental change, in order to complete all the required activities to sustain life and reproduction (Hill, 2006a). Díaz et al. (2006) demonstrated that for large psammodromus (*Psammodromus algirus*), a lizard native to the temperate regions of Europe, a change in their preferred thermal range (PTR) during different seasons is directly related to species fitness. During spring, the breeding season, the lizards chose lower environmental temperatures within a thermal gradient established under laboratory conditions. However post-breeding season, during summer, they did not actively thermoregulate and chose higher environmental temperatures that were closer to their PTR. This behaviour was explained by conformity to seasonal shifts in photoperiod and maintaining optimal PTR to facilitate top sprint speed, which has a direct impact on individual fitness. Furthermore, females in particular may behaviourally thermoregulate during spring, as this is the peak of the reproductive period, and there may be a physiological benefit to maintaining a lower PTR whilst carrying eggs (Díaz et al., 2006).

Similar behaviour patterns can be detected in mammals. Lynch et al. (1973) observed that when white-footed mice (*Peromyscus leucopus*) were exposed to short photoperiods, under laboratory conditions, they were less active and their activity was focused towards thermoregulation and winter survival. *In situ* observations of two pika (*Ochotona princeps*) populations by Smith (1974) at two different altitudes in California revealed altitude was a proxy for temperature and had a dramatic effect on pika behaviour. The population living at a lower altitude, and therefore experiencing higher temperatures, had a bimodal activity profile with an early morning peak followed by a late afternoon peak. Behaviours including hay storage, vocalisations and parturition all occurred 6 weeks earlier at lower altitude, whereas the high altitude population showed little effect from temperature or seasonality. Hay storage and vocalisations were both correlated with winter rainfall with a dry winter and early spring prompting the pika to begin and end their hay storage and vocalisations earlier than if they had experienced a wet winter and late spring. Pikas

have a larger range and occupy a wider variety of sites at higher altitudes. These findings indicate pikas are affected by heat stress at low altitudes due to their heavily insulating fur and poor thermoregulatory abilities.

Hyraxes, like pikas, have additional pressures placed on them when the season changes, as they too are unable to adequately thermoregulate. Sale (1970) conducted a study on two groups of free living hyrax (*Procavia* and *Heterohyrax*) measuring both the ambient air temperature and rectal temperatures from a number of individuals simultaneously. The result showed that there is an approximate relationship between the ambient temperature and the body temperature of hyrax and places them on the scale between true endothermic mammals and poikilothermic reptiles and amphibians. The energetics of being endothermic are influenced by a number of factors, and McNab (1974) concluded body size, climate and diet all combine to control the endothermic capacity of an animal. Body size determines an animals' basal metabolic rate and their thermal conductance which when combined establish a temperature differential between the animal and its environment at the lower threshold of thermoneutrality that typically increases with body weight. Climate has a direct effect on both the temperature differential between the environment and the animal and the animals' quantity and availability of food. McNab (1974) also explains that an animals' thermal conductance is a product of its surface-to-volume ratio and the surface-specific insulation and this thermal conductance can be altered depending on climate of the area, for example: arctic species have a low thermal conductance as do temperate species during the winter months. However, lowland species have a much higher thermal conductance, as do temperate species during the summer months, as maintaining body temperature in line with the environmental temperature, increasing thermal conductance, is the most efficient way to control body temperature. For food habits or diet, it can be concluded *a priori* that diet would influence the role of energy and, therefore, endothermic temperature regulation. Endotherms may be limited to warm climates due to maintaining high metabolic rate or could be physiologically limited to how much food they can consume at any one time as is the case with vampire bats as they are limited by the largest meal they can carry whilst in flight (McNab, 1973).

For hyraxes, this means that during winter and summer, where they experience temperature extremes, they must behaviourally thermoregulate by physically relocating to an environment where the temperature is within their thermoneutral zone. The other behaviour they use to compensate during extremes of temperature is inactivity. This helps because they are able to slow down their metabolism and by remaining inactive they use considerably less energy, allowing their bodies to adjust to the ambient temperature without any lasting detrimental effects (Sale, 1966a). Sale (1970) reports that throughout constant observation periods in the field adult hyrax were recorded inactive 95% of the time.

The predicted effect of extreme variation between the wet warm summer season and the cool dry winter season should present significantly different activity profiles. It is hypothesised that in winter hyrax will need to be active during the middle of the day as temperatures will be at their highest. Contrastingly, in summer we would expect a bimodal activity profile where hyraxes are actively avoiding the hottest part of the day, being active early morning and late afternoon. These profiles would utilise the most appropriate environmental temperatures and satisfy the need for adequate solar energy for behavioural thermoregulation throughout the year.

Hypothesis:
H_0: There is no difference in activity patterns of hyrax between the four seasons that occur in the Soutpansberg Mountains.

H_1: There are significant differences in activity patterns of hyrax between the four seasons: in particular, between cool dry winter where activity should be constant between sunrise and sunset and warm wet summer where activity may be lower during the middle of the day, giving a bimodal activity pattern.

Site specific activity

Most animals require varied resources in their habitat in order to satisfy their daily requirements of food, shelter and social interaction. For some animals this can only be maintained by travelling large distances; many bird species choose to migrate for breeding and dietary requirements (Dingle, 1996; Gauthreaux, 1996), large herds of migratory herbivores utilise alternative food sources (Fryxell, 1995; Murray, 1995) or whales that migrate to avoid predation (Corkeron and Connor, 1999). In an ideal world, animals would choose the path of least resistance that easily leads them to habitats with a variety of characteristics allowing them to carry out their daily activities. However, certain factors within an animals' habitat can affect their behaviour more severely than others. Downes and Shine (1998) evaluated the effects of temperature, sociality and predation risk on the velvet gecko (*Oedura lesueurii*). Within a laboratory environment they demonstrated that seeking shelter (retreat-site selection) was influenced by thermal benefits, social advantages and predator avoidance, however all these factors were weighted differently and had to be prioritised in the presence of conspecifics. When in competition, the bigger and more dominant geckos obtained warmer retreat-sites and when predator scent was applied to various sites the more dominant animals out-competed the smaller subordinate geckos for the non-predator-scented sites. In general, predator avoidance was a higher priority than thermoregulation as all geckos chose cooler predator-free retreat-sites in favour of warmer predator-scented retreat sites. The priorities appear to be the same for mammals, as *in situ* observations of the Southern ningaui (*Ningaui yvonneae*) showed that hummock grass (*Triodia irritans*) was the preferred habitat overall as it

consists of densely packed clumps of sharpened spikes and it is believed to offer the best protection from predators. Leaf litter was favoured when foraging, possibly due to greater energetic returns. However, when foraging in leaf litter the ningauis remained close to hummock grass and even took large prey items into the hummock grass to be consumed, demonstrating that habitats offering the greatest protection from predators are consistently favoured over those that yield other benefits, such as higher energetic yield or thermoregulatory benefits.

Hyrax have been shown to be central place foragers (Kotler et al., 1999). This behaviour is characterised by a more thorough foraging effort in the area surrounding the animals central place such as a burrow or water source (Orians and Pearson, 1979). Whether an animal can maintain this behaviour is influenced by many things such as the presence of competitors and food supply, especially if food availability is seasonal and load size of food must be transported back to the central place (Giraldeau et al., 1994). In the case of hyrax the main influences on central place foraging are distance from central place/koppie (rocky outcrop) and risk of predation, demonstrated by their favouring of covered locations when interacting with artificial food patches (Druce et al., 2006; Kotler et al., 1999). Foraging behaviour of hyrax, in an environment where predators were present, documented by Fourie and Perrin (1989) describes a unique behavioural pattern, involving hyrax leaving the home range/koppies individually, at a staggered rate, and spreading out to cover large areas. It has been suggested by Fourie (1983) that this is because single animals attract less attention from predators and the animals can forage across a larger area by all remaining vigilant and therefore sounding the alarm early if a predator is detected. However other published studies showed a distinct bimodal daylight group foraging pattern (Hoeck, 1975; Sale, 1965a). This flexibility in behavioural pattern for foraging and could be resource and threat dependant. If the resources are exceptionally good and the predation threat is deemed relatively low, then the group foraging twice daily could be beneficial to all individuals within a group. In contrast, if the resource quality is low and the predation risk is high then the solitary foraging behaviour described by Fourie and Perrin (1989) may be more likely to be observed. The most beneficial behavioural profile would be one of constant flexibility, as the surrounding habitat is a dynamic system that needs to be constantly reassessed by the hyrax. Furthermore, foraging hyrax have been known to utilise sentinels to observe for possible threats and notify the colony, by alarm calling, when a threat is detected which could also affect the behavioural profile when foraging (Druce et al., 2006; Fanson et al., 2011; Kotler et al., 1999). This combined with the security of rock crevices and a flexible and variable diet could be major contributing factors to the survival of a prey species such hyrax.

For hyrax, activity can be broken down into many categories including travelling, resting, mating, basking, foraging, socialising and defecating (Barry and Mundy, 2002; Brown and Downs, 2007;

Canady, 2012; Olds and Shoshani, 1982; Sale, 1970). All of these behaviours require a specific combination of environmental variables to be carried out. For this study five categories, resting, basking, foraging, travelling and socialising, were chosen as a focus for analysis as these categories cover the majority of hyrax behaviours and may be the most influenced by weather and habitat variation (Sale, 1965a; Sale, 1966b, 1970; Taylor and Sale, 1969). Resting typically takes place on or inside the koppie (or rocky outcrop) inhabited by the hyrax. Resting is the most common behaviour and takes place out of direct sunlight either in a group, where the hyrax are heaping or huddling, (Sale, 1970) or individually depending on the ambient temperature. Hyrax will rest both when they are hot or overheating (typically individual animals) but also when they are trying to increase their body temperature (by huddling or heaping together as a group). Basking, on the other hand, is when the hyraxes actively seek out direct sunlight and lie in it, often spread out and dorsally flattened, either as part of a group or as individuals.

Travelling is a risky behaviour for a prey species (Eccard and Liesenjohann, 2008; Lima et al., 1985) but it is particularly risky when using roads and trails as this is a favoured method for predators to navigate their territory (Forman and Alexander, 1998). Benítez-López et al. (2010) showed that there was an increase in activity from raptors near roads due to high levels of carrion, as well as live prey. Mammalian predators use roads too, in particular large predators as Martins and Harris (2013) showed with the larger male leopards used roads significantly more than their female counterparts. Some predators are a little more specific with their use of roads, as wolves (*Canis lupus*) in North America were shown to use areas within 25 metres of roads trails and railways with higher frequency, however, they preferred low use road and rail networks rather than high use busy infrastructure. Cougars also showed a preference for quieter dirt roads, avoiding two lane sealed roads, and utilised less rugged travel paths compared to general surroundings when hunting or travelling (Dickson et al., 2005). A camera trap study in Belize, South America found that predator specific photographic trap success positively correlated with width and or length of roads, with ocelot (*Leopardus pardalis*) and jaguar (*Panthera onca*) showing the biggest preference for roads, puma capture rate correlating with road width and jaguar and ocelot correlating with road length (Davis et al., 2010).

Hyraxes are known to have a varied diet (Sale, 1965a; Sale, 1965c, 1966a) so foraging can be conducted anywhere suitable food can be found, but rock hyrax are not adept at climbing so food sources must be at a suitable height. Rock hyraxes have been shown to vary the duration of foraging sessions depending on habitat type. Meltzer (1973) studied the Syrian rock hyrax (*Procavia capensis syriaca*) and showed that those populations foraged for up to three or four hours a day in order to satisfy their energetic requirements. However, Sale (1965a) presented observations on rock hyrax in the Serengeti, Kenya and suggested that those populations could fill their stomach with an hour

of continuous foraging. The two foraging behaviours could be influenced by habitat type or food availability as both have been shown to influence hyrax foraging behaviour (Druce et al., 2006; Kotler et al., 1999).

From the limited studies of rock and bush hyrax behaviour there appears to be considerable variability throughout their range and that additional information, particularly from a predator rich environment, is a valuable contribution. A null hypothesis of no effect of habitat type on the behaviour recorded will likely be rejected in place of a strong relationship between habitat types and behaviours recorded.

Hypothesis:
1. H_0: There is no effect of habitat type on the activity pattern of hyrax.

   H_1: There is a strong relationship between habitat type and the activity pattern of hyrax.

2. H_0: There is no correlation between the activity recorded and the weather conditions.

   H_1: The level of basking activity recorded increases as the minimum overnight temperature decreases.

   H_2: Rainfall has a negative effect on the level of activity of hyrax in the Soutpansberg Mountains.

Methods

The study was conducted at the Lajuma Research Centre located in northern South Africa within the western Soutpansberg Mountains, Limpopo Province, South Africa (23°02'17.1"S 29°26'26.5"E) (Chapter 2: Figure 2.5). This study examined two species of hyrax that both inhabit the study site, and in several locations, were observed living in sympatric colonies. Therefore, herein the two species will be grouped and referred to as hyrax. See Chapter 2 for comprehensive information on the location of the study and species description.

Data collection

A group of 13 cameras were erected at eight sites to monitor hyrax activity (see Chapter 2 Methodology: Table 2.2 for camera information). These cameras collected a total of 6174 images of hyrax. The second camera array run by the Primate and Predator Project (PPP) encompasses a large proportion of the Soutpansberg Mountain range. The images obtained from this grid span 3.75 years and these cameras collected a total of 4193 images of hyrax.

Data analysis

Seasonal variation in hyrax activity during daylight hours

For continuity, when investigating seasonal variation in hyrax activity during daylight hours only data collected from the Primate and Predator Project cameras was used. The computational procedure used for the overlap analysis within this chapter followed the same protocol as in Chapter 3. To compare the shape of the activity profiles between seasons the density of activity for each of the four seasons was divided into 5% intervals across the hours of daylight (sunrise to sunset). In this analysis, the data were split into four seasons (see Chapter 2: Data analysis for definitions). However, when comparing and contrasting the weather conditions and activity profiles of hyrax for the four seasons, spring and autumn can also be classed as the transitional periods as shown in other ecological studies conducted in the area (Chase-Grey, 2011a; Kabanda, 2003) or grouped together into summer and winter as in Tambling et al. (2015) who categorised only two seasons within the Addo National Park, South Africa with winter occurring from 16th of March until the 27th of September and summer from the 28th September until the 15th March.

General Linear Modelling (GLM) was implemented to test the seasonal hypotheses relating to temperature and rainfall. The density of activity of hyrax across the 24-hour period from the overlap analysis for each season was extracted by creating an object containing the density of activity from the densityPlot function within the Overlap package (Ridout and Linkie, 2009). The density of

activity, extracted in 15 minute intervals across the 24-hour period, were then averaged to 30 minute intervals to match the temperature readings obtained from the South African Environmental Observation Network (SAEON) affiliated weather station at the Lajuma Research Station. Since the relationship between temperature and activity may be non-linear, a quadratic temperature term was included in the models to determine if it improved model fit.

Behavioural analysis

Analysis of specific behaviours and their associated activity profiles was conducted on the images collected from the hyrax cameras. These images were subsequently tagged with a behavioural code informing the number, age and behaviour of all animals within the image. The mean behavioural profile for each 30 minute time interval was then computed, to allow direct comparison with the weather data.

From these behaviour profiles, it was hypothesised that basking may show a relationship with minimum overnight temperature so the relationship was plotted and tested using a Pearson's correlation. A further hypothesis on the effect of rainfall on activity was also tested by plotting average rainfall against the number of images captured and by transforming rainfall into a discrete variable, a Mann-Whitney U test of differences was used to conduct an initial coarse scale analysis to determine if activity differed during high versus low rainfall. Subsequent analysis aimed to discern the main factors influencing the proportion of time hyrax spent resting and basking. The behavioural data was made proportional (bounding it between 0 and 1) and a multivariate test in the form of a general linear mixed-effects model (GLMM) was used. Parameters included in the model for proportion of time resting were maximum daytime temperature, rainfall, Julian day with site as a random effect. For proportion of time basking the parameters were mean daytime temperature, rainfall, Julian day with site as a random effect. The models were run using the glmer command with family specified as binomial, within the 'lme4' package (Bates et al., 2015) in the statistical software program R (R Core Team, 2014).

Overlap: Site specific activity

Overlap (see Chapter 2: Data analysis for detailed description of R package) was implemented to generate activity density profiles to investigate site specific activity using both sets of cameras data. Due to the two different camera arrays, an initial visualisation of the activity patterns was done to

investigate the differences between the roadside cameras from the PPP array and the site specific cameras from the hyrax array. The sites were then consolidated using habitat type or behavioural category: e.g. roads and trails, cliff, woodland, manmade (Barn) and latrine sites.

Results

Hyraxes within the Soutpansberg Mountains have a predominantly diurnal activity pattern with 91.6% of activity occurring within the hours of daylight (Figure 4.1). This pattern is largely unimodal, with activity beginning at 05:30 and increasing incrementally until it peaks at about 17:00, before a steep decline in activity to low levels of activity throughout the dark period of the 24-hour cycle.
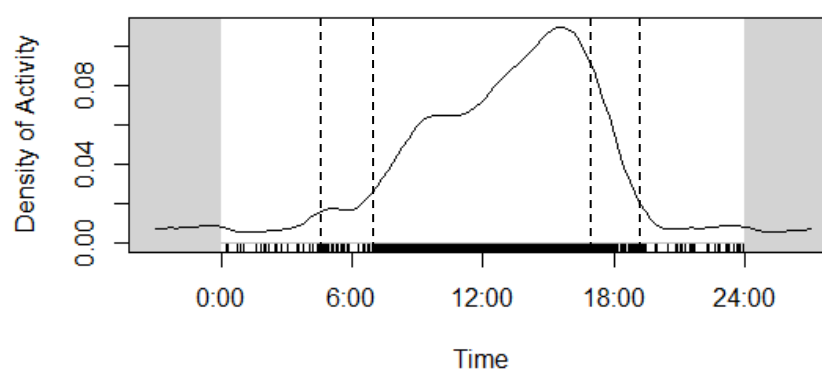
Figure 4.1: Diurnal activity pattern of hyrax within the Soutpansberg Mountains across all seasons and habitats. The dotted lines indicate the change in sunrise and sunset across the year. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Seasonal variation in hyrax activity during daylight hours

Variation exists in the activity profiles between seasons. In particular, when comparing the activity profile for hyrax during the summer (wet warm season) months with that of the winter (cool dry season), the activity patterns are markedly different with an estimation of overlap of 59% (Figure 4.2 (top)). In winter, a bimodal pattern of activity is evident that begins at approximately 07:00 and ends at about 18:00; this contrasts with a slow build in density of activity in summer. The summer activity is also bimodal, but the first peak at dawn (06:00) is disproportionately smaller than the second peak occurring at 18:00. Spring and autumn demonstrate very similar activity patterns with an estimation of overlap of 74%; spring could be classed as a bimodal activity profile but the first peak is minor and autumn has a largely unimodal activity profile with only an afternoon peak at 18:00 (Figure 4.2 (bottom)).
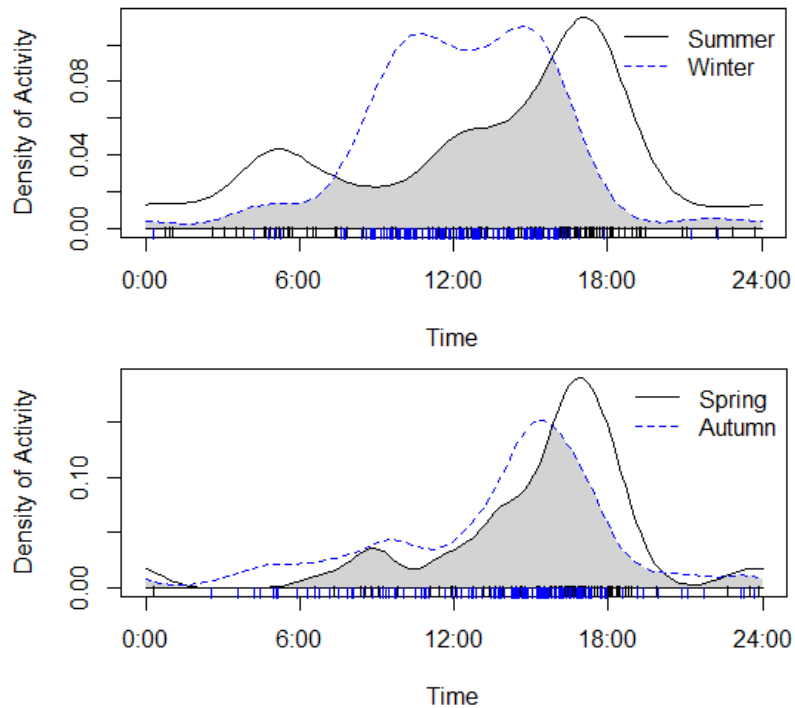
Figure 4.2: The density of activity of hyrax across the 24 hour period, throughout summer and winter (top) and throughout spring and autumn (bottom). Both figures use only the Primate and Predator Project data set. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

It is clear that the shape of the activity pattern in winter is different to that of spring, summer and autumn (Figure 4.3), and while the activity profile for winter does correlate with that for autumn (Table 4.1), the strongest positive correlations were between summer with spring and autumn indicating the greatest similarity in activity pattern between these seasons. This is because winter is a bimodal activity pattern centred in the middle of the day whereas summer, autumn and spring are primarily skewed toward the later part of the day into the early evening.
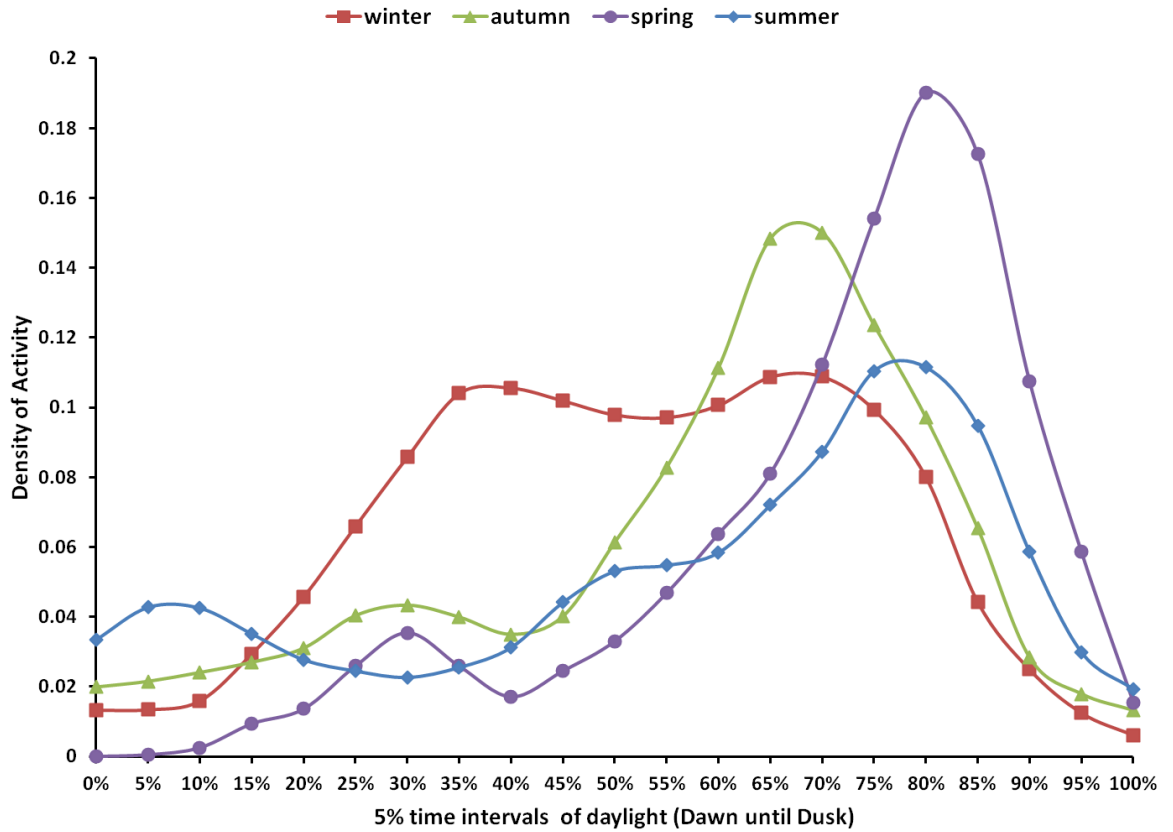
Figure 4.3: Density of activity of hyrax from dawn to dusk across all four seasons, broken down into 5% time intervals from dawn until dusk. Data selected from images captured by the Primate and Predator camera trap grid only.

Table 4.1: Pearson's rank correlation (r) of seasonal activity patterns comparing the activity profiles of hyrax between winter, spring summer and autumn (Figure 4.3). Levels of significance are shown as ** = $p < 0.001$; * = $p < 0.01$.

	Summer	Winter	Autumn	Spring
Summer		r = 0.34	r = 0.75**	r = 0.90**
Winter	r = 0.34		r = 0.70**	r = 0.27
Autumn	r = 0.75**	r = 0.70**		r = 0.63*
Spring	r = 0.90**	r = 0.27	r = 0.63**	

Winter is best explained as a linear relationship with temperature (r^2=0.410, $F_{(1,21)}$ = 16.27, p < 0.001) while quadratic relationships best account for the relationships in spring, summer and autumn (spring: r^2=0.721, $F_{(2,23)}$ = 33.35, p < 0.001; summer: r^2=0.849, $F_{(2,25)}$ = 76.03, p < 0.001; autumn: r^2=0.845, $F_{(2,22)}$ = 60.04, p < 0.001). In all cases activity was substantially higher at high temperatures (Figure 4.4). While expected for winter, the highly significant positive relationships for spring, summer and autumn contrasted with the initial predictions.

Winter
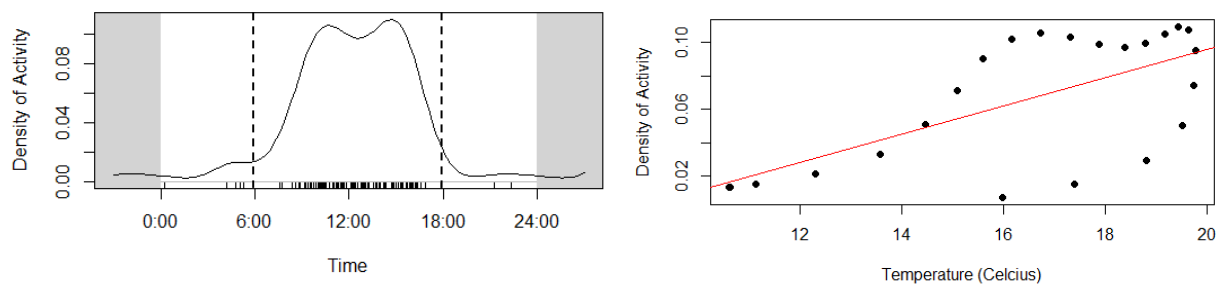
Spring
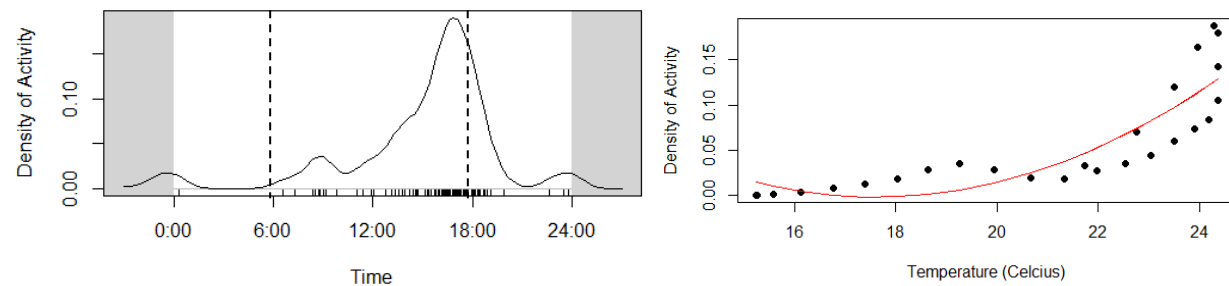
Summer
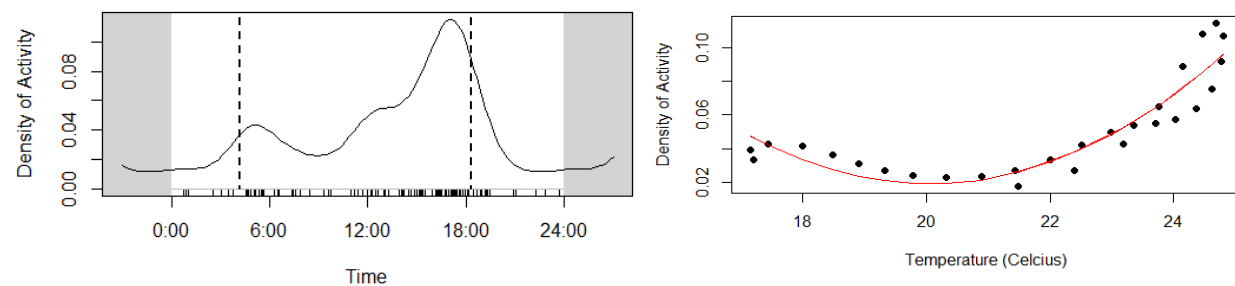
Autumn
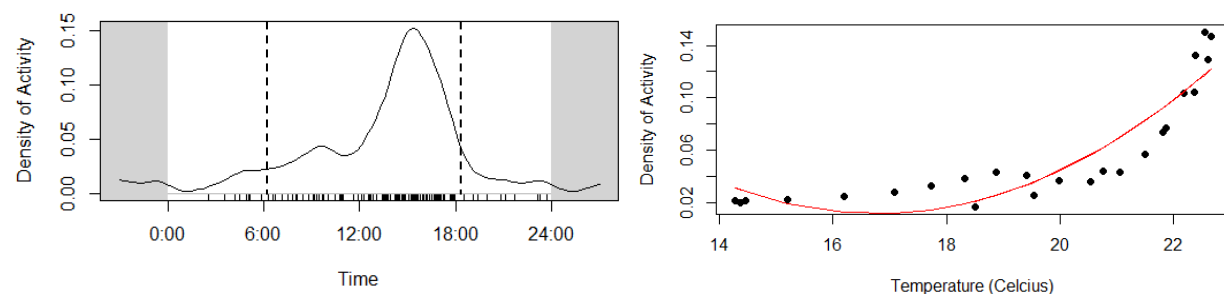
Figure 4.4: The plots on the left show the seasonal activity profiles with dotted lines indicating sunrise and sunset. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed and the grey bars on the left and right indicate that the data is circular across the 24-hour period. The plots on the right are density of activity of hyrax plotted against the daytime ambient temperature between sunrise and sunset for each season with a line of best fit from a general linear model. All figures use only the Primate and Predator Project data set.

When testing the hypothesised effect of rainfall on the density of diurnal activity of hyrax the relationship is very different to that of temperature and activity (Figure 4.5). Generalised linear models revealed that rainfall has no significant effect on density of activity of hyrax across seasons (winter: $r^2 = 0.046$, $F_{(1,21)} = 2.05$, $p = 0.167$; spring: $r^2 = 0.003$, $F_{(1,24)} = 1.08$, $p = 0.310$; summer: $r^2 = -0.026$, $F_{(1,26)} = 0.32$, $p = 0.574$; autumn: $r^2 = 0.109$, $F_{(1,23)} = 3.92$, $p = 0.060$).
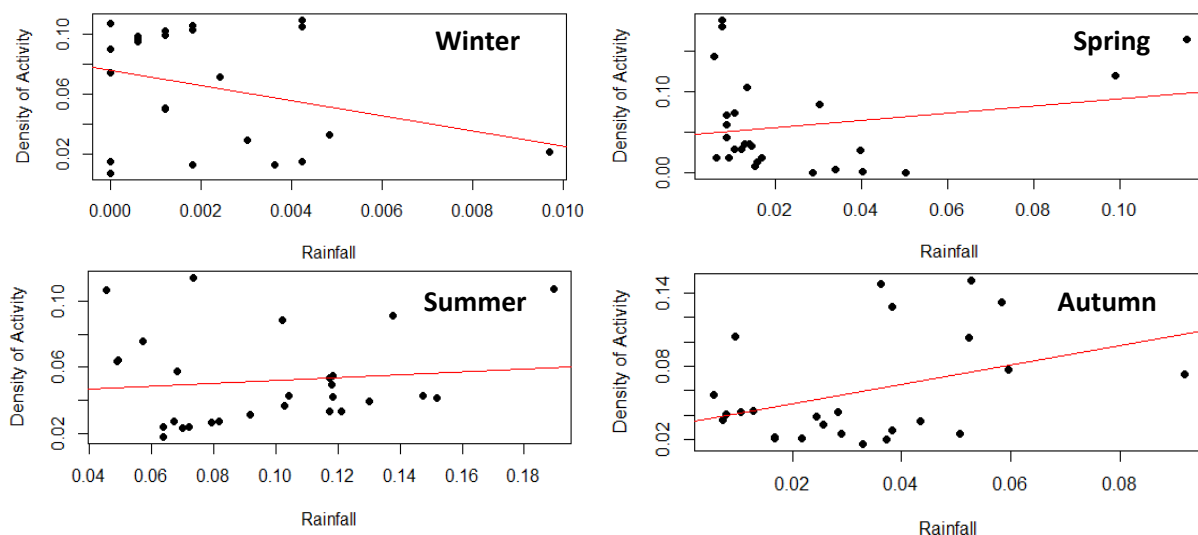
Figure 4.5: Density of activity of hyrax during the hours of daylight plotted against rainfall in mm during the same time period for each season. From left to right: winter, spring, summer, autumn.

Behavioural analysis

The proportions of behaviours detected in the data from the hyrax camera array are detailed in Table 4.2. Resting, travelling and basking are clearly the three most frequent behaviours recorded in images for hyrax inhabiting the study site, and the next analyses focus on these activities.

Table 4.2 Breakdown of activities detected within camera trap images collected from the hyrax camera array.

Behaviour	Resting	Basking	Foraging	Travelling	Socialising
Percentage of total activity recorded	39.40%	28.50%	0.48%	31.04%	0.60%

The patterns of the three main behaviours exhibited by hyrax shows clear distinction between basking and travelling with the former occurring between the hours of 06:30 and 16:30. Travelling is the dominant behaviour between the hours of midnight and 05:00 and then again from 20:00 until midnight. Resting shows a similar profile to basking but the beginning and end of the activity

profile are less well defined with some resting animals observed during darkness. Since changes in behaviour are likely to occur in response to the environment, weather conditions may constrain the patterns of activity observed.
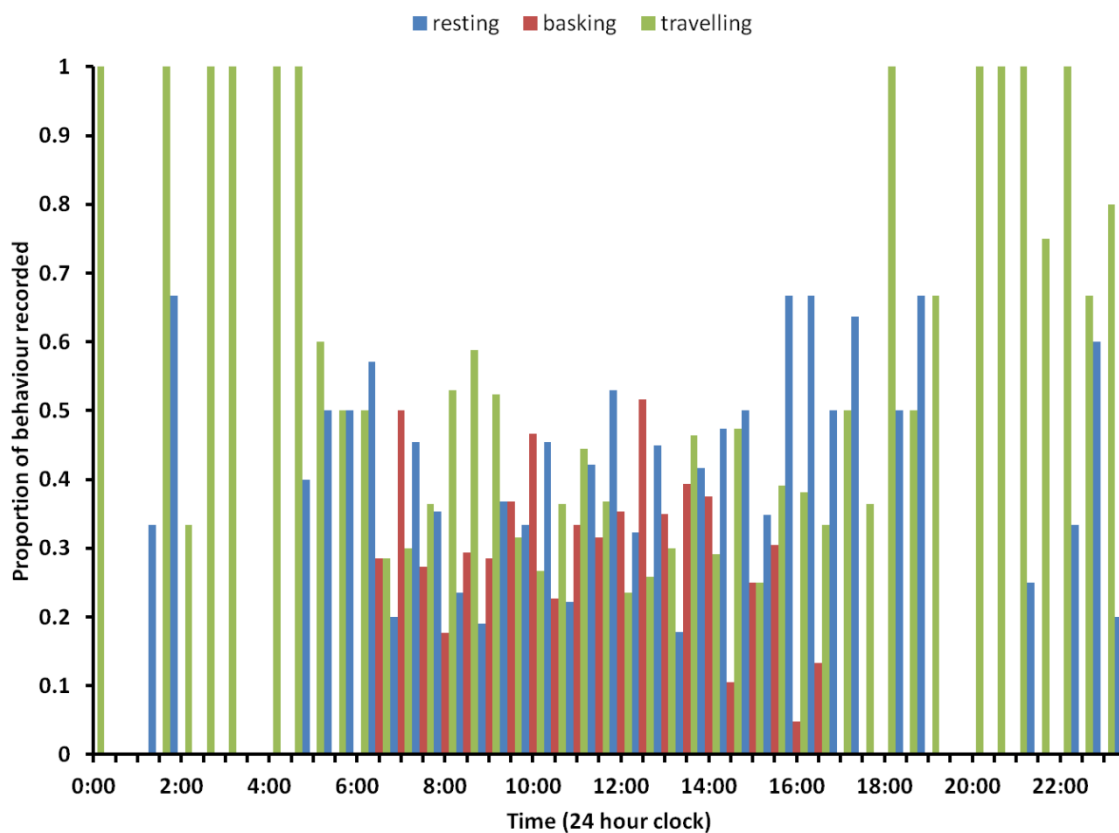
Figure 4.6: Resting, basking and travelling behaviours shown by hyrax quantified across the 24-hour period. Proportion of behaviour recorded on the y axis is the number of images within a 30 minute period in which the behaviour was recorded divided by the total number of images recorded within that 30 minute period.

The impact of rainfall on the temporal pattern of activity of hyrax can be seen in Figure 4.7 where a summary plot of mean number of images on days with or without rain shows that there is a significant effect of rainfall on level of activity but the standard deviation of the mean is also high, showing variability within these two categories (Figure 4.7). A Mann-Whitney U test confirmed rain has a significant influence on the activity profile of hyrax ($p < 0.001$), with hyrax largely out of sight on days with rainfall. By quantifying resting behaviour and modelling it along with minimum temperature and rainfall, accounting for date and classing site as a random effect it is clear that the number of animals resting is affected by date with rainfall approaching significance and site accounting for 0.7% of variance within a generalised linear mixed-effects model (Table 4.3).
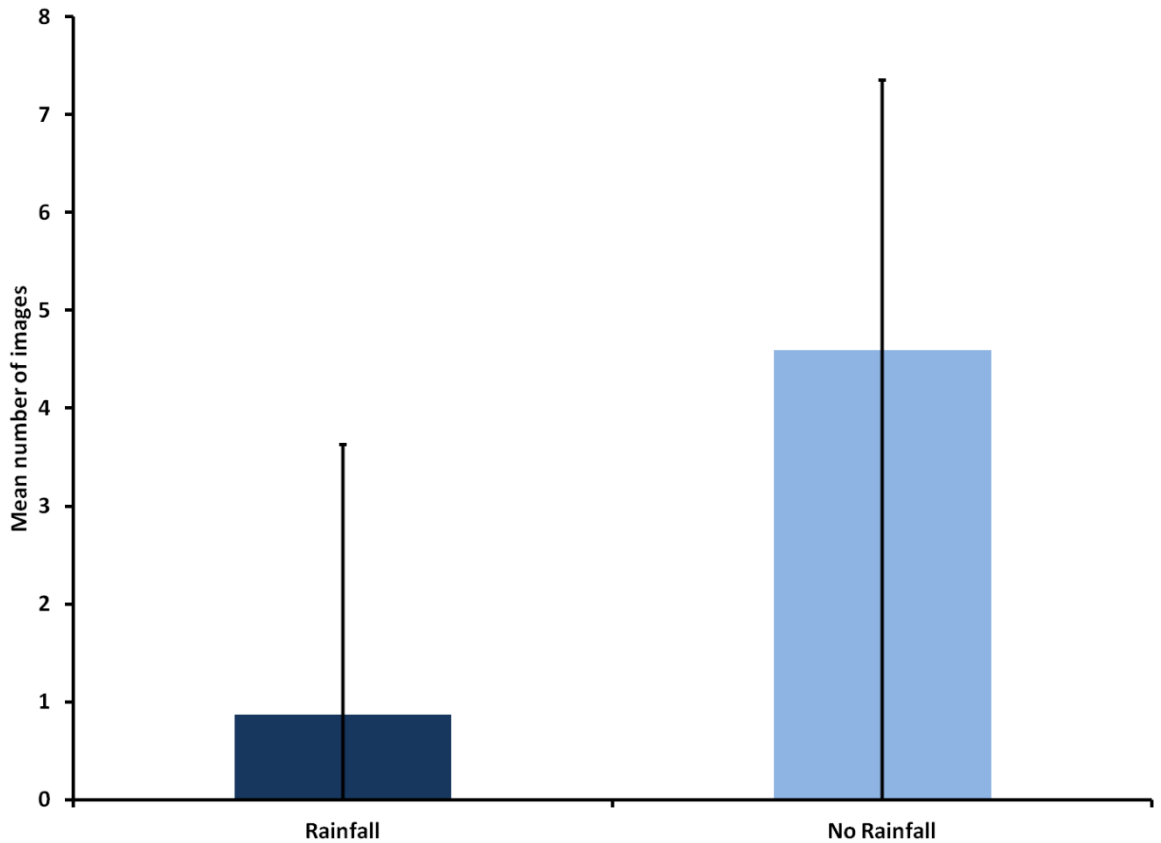
Figure 4.7: Column graph showing mean number of images captured per day with and without rainfall with SD error bars. Mann-Whitney U test of differences: V = 1953; p < 0.001.

Table 4.3: Statistical summary of the general linear mixed-effects model examining the relationship between proportion of animals resting and maximum daytime temperature, rainfall, Julian day with site as a random effect. Note: Family within model structure set to binomial as response variable is bounded by 0 and 1.

Model: Proportion of animals resting ~ maximum daytime temperature + rainfall + Julian date + (1|site)				
Random effects				
	Variance	**Standard deviation**		
Site	0.71%	0.84%		
Fixed effects				
	Estimate	**Standard error**	**z value**	**p value**
Maximum temperature	-0.02	0.07	-0.32	0.751
Rainfall	13.94	7.51	1.86	0.063
Julian date	-0.02	0.01	-2.39	0.017

When testing the hypothesis that minimum overnight temperature could influence basking activity on the following day there was a negative correlation between the minimum overnight temperature and the basking behaviour recorded the following day (Pearson's correlation: r = -0.24, n = 76, p = 0.04) (Figure 4.8). Thus, basking increases after cold nights. When basking behaviour

was tested for its relationship to average daily temperature and rainfall within a generalised linear mixed-effects model (Table 4.4) that accounts for the effect of date and includes site as a random factor neither temperature nor rainfall is significant. Both approach statistical significance suggesting possible cumulative effects on the number of animals basking. Site, as a random effect accounted for 23.3% of the variance within the model, suggesting that the features relating to the location of the camera may also be important in determining activity.
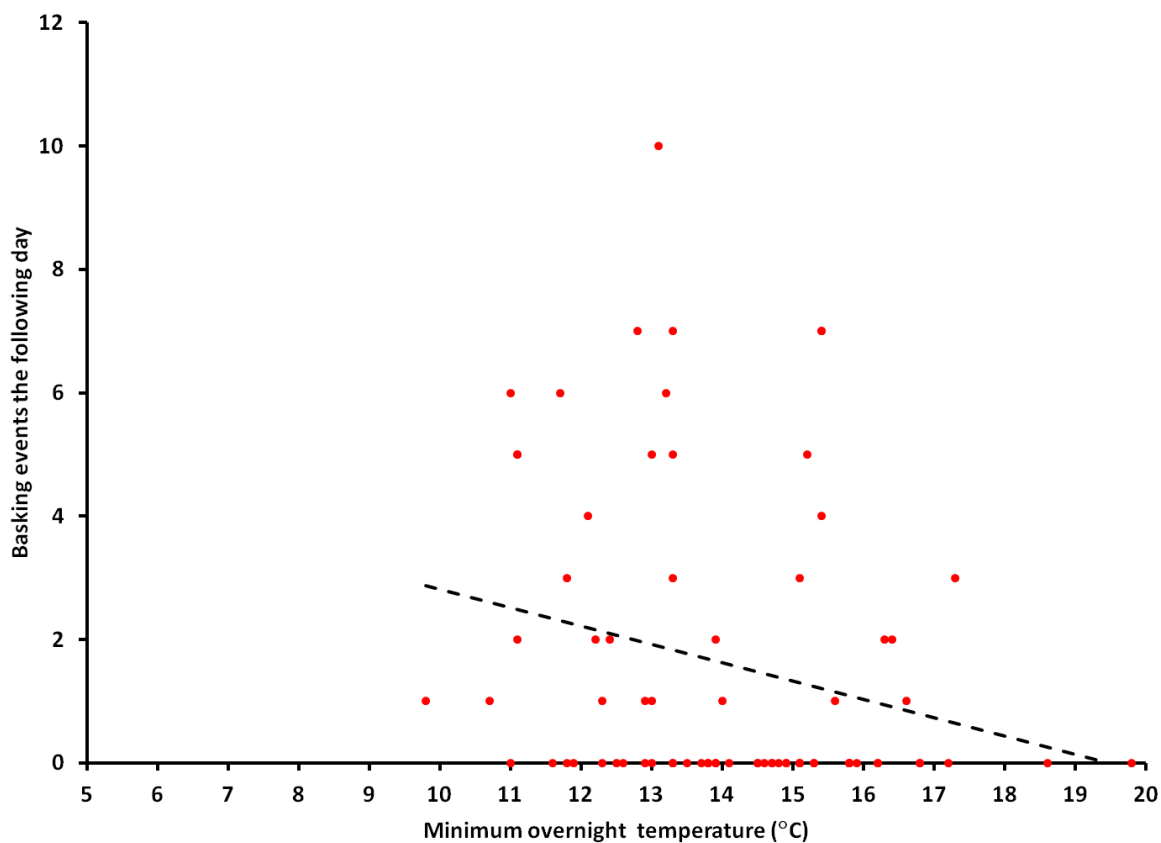
Figure 4.8: Minimum overnight temperature (°C) plotted against number of basking events recorded the following day with a line of best fit for visual interpretation only as the relationship is not linear. Number of basking events was determined by the number of times basking behaviour was recorded across the day (Pearson's correlation: r = -0.24; t = -2.11; df = 73; p = 0.04).

Table 4.4: Statistical summary of the general linear mixed-effects model examining the relationship between proportion of animals basking and mean daytime temperature, rainfall, Julian day with site as a random effect. Note: Family within model structure set to binomial as response variable is bounded by 0 and 1.

Model: Proportion of animals basking ~ mean daytime temperature + rainfall + Julian date + (1|site)				
Random effects				
	Variance	**Standard deviation**		
Site	23.3%	4.8%		
Fixed effects				
	Estimate	**Standard error**	**z value**	**p value**
Mean daytime temperature	0.15	0.082	-1.79	0.073
Rainfall	-44.24	38.22	1.79	0.074
Julian date	-0.008	0.01	-0.78	0.435

Site specific activity

To test the hypothesis of site specific effects on activity the first comparison was of two sets of images from the same site collected at different times. By overlapping the Louisville activity profile (collection dates: 8th of March 2015– 17th of May 2015) with the activity profile from PPP station 18a (collection dates 26th August 2011 – 1st of August 2013) it resulted in an estimation of overlap between these two sites of 84% (Figure 4.9). This demonstrates that cameras placed in certain locations produce remarkably consistent data over time suggesting that activity profiles obtained from different cameras can produce reliable estimates of site-specific activity.
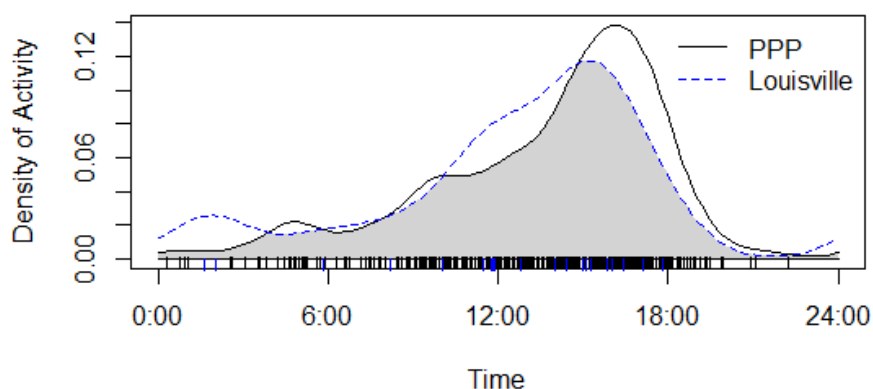
Figure 4.9: Density of hyrax across the 24-hour period for the same location, Louisville/PPP Station 18a, measured across two different time periods (see Figure 2.12 for exact location within field site). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

The consequent question from the analysis in Figure 4.9 is that of the effect of landscape scale habitat types on activity patterns of hyrax in the Soutpansberg Mountains. A feature of these mountains is the high diversity and mosaic of habitat types and so different locations may give rise to different activity profiles based on the local conditions. For example, there is clear differentiation in sites used for locomotion versus basking, feeding or defecating (Figure 4.10). Another feature of the study site is its unsealed road and trail network. the impact of this feature is clearly seen in a comparison of PPP sites and hyrax sites where PPP cameras are located on roads and trails and hyrax cameras are away from roads and trails. This presents a big difference in activity profiles with road and trailside sites delivering a skewed unimodal peak that showed the majority of activity occurring between the hours of 12:00 and 18:00 whereas the hyrax specific cameras detected a more centred unimodal peak beginning at approximately 06:00 and continuing through until 18:00 (Figure 4.10: Road and trailside sites and all other sites).

Cliff habitats are important in hyrax ecology so the question was posed about the visitation level of these sites throughout the day. The cliff habitat type shows a similar unimodal activity profile to the road and trailside sites with the peak of activity seen to begin at midday and continue until 17:00 (Figure 4.10: Cliff sites). To understand the types of sites the hyrax visited throughout the day woodland sites were also examined. The hyrax activity profile from these woodland habitats shows a distinctly bimodal profile with an early and wide peak that begins at 10:00 and drops off at 16:00 before increasing again to a smaller narrower peak at 18:00 (Figure 4.10: Woodland sites).

It was further hypothesised that basking behaviour (Figure 4.8) may be connected to specific sites, particularly those with extensive direct sunlight, and as a consequence this would influence the levels of activity detected in these areas. Indeed, basking sites do have a distinctive activity profile which is comprised of exclusively diurnal activity that begins sharply at 07:00 is consistently high until it abruptly ends at 18:00. This is partially in line with the activity profile of basking from Figure 4.6 but Figure 4.10 does show basking behaviour continuing past 16:30 which is logical given the data in Figure 4.10 covers basking behaviour throughout the year from both camera arrays and Figure 4.8 was restricted to the hyrax camera array and therefore the winter months (Figure 4.10: Basking sites).

Road and trailside sites and all other sites
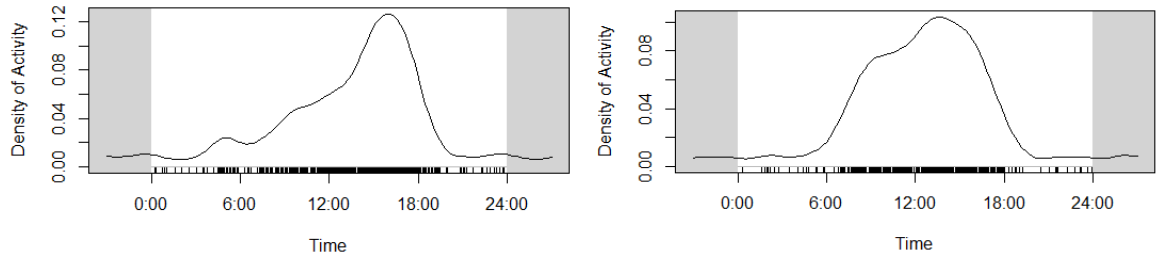
Cliff sites
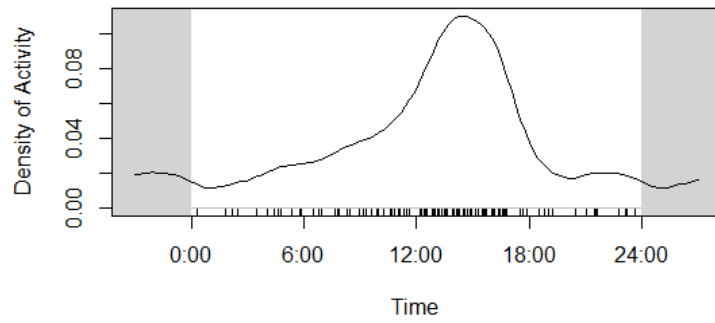
Woodland sites
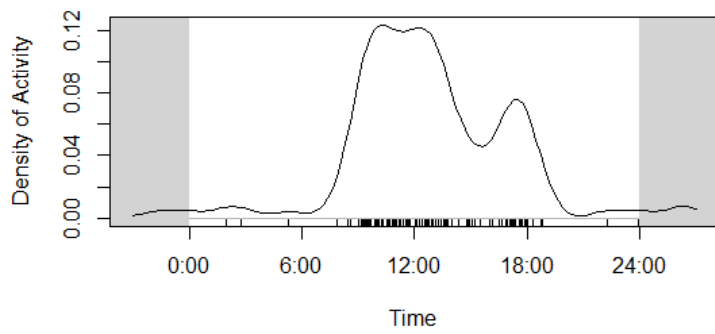
Basking sites
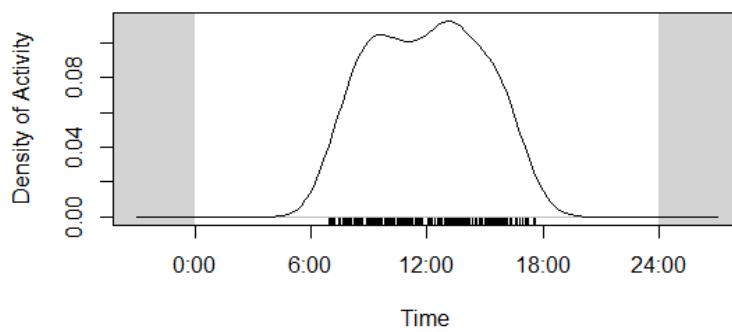
Figure 4.10: Site specific activity profiles for road and trailside sites (left) and all other sites (right), cliff sites, woodland sites and basking sites. The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Figure 4.10 highlights that different camera locations can generate different activity profiles based on the function of those regions for hyrax ecology. Nevertheless, distinct behavioural profiles can be developed from cameras placed in close proximity highlighting the potential importance of micro-habitat features in generating the activity profiles. For example, two locations at the Barn site show that there is indeed the potential for major differences in activity patterns to occur within similar locations (Figure 4.11). The Barn site had a small colony of hyrax residing in the woodland surrounding a group of buildings and the two cameras were within approximately 20 metres of each other. Nevertheless, the estimation of overlap of the activity profiles was just 25% revealing that the two locations within this site are used at different times throughout the 24-hour period. In particular, the latrine site had a highly skewed pattern of activity, differing significantly from the fence site that was used predominantly for basking.
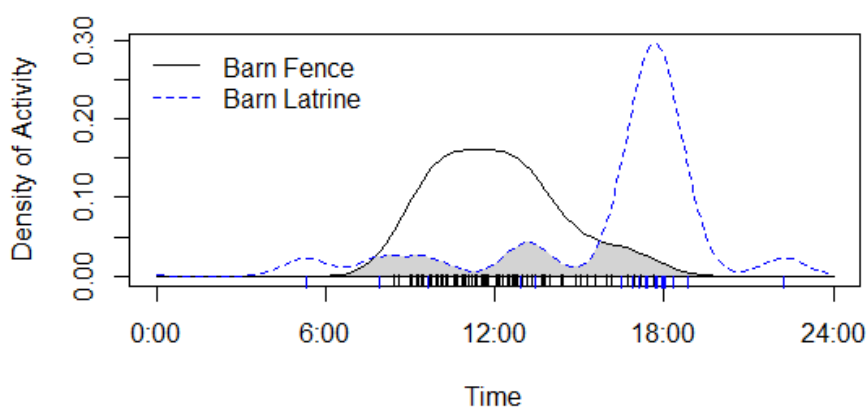
Figure 4.11: Density of hyrax over the 24-hour period from two cameras located at the manmade Barn site (see Figure 2.12 for exact location within field site). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

While these results suggest that cameras may be able to accurately identify site functions from behavioural profiles, it is important to recognise that not all latrine sites produced such distinctive profiles. Activity at the second latrine site showed inconsistent patterns of activity with a slow rise across the day that contrasted markedly with the Barn latrine showing a more distinct peak (Figure 4.12). While cameras thus offer an important window into animal behaviour they nevertheless require a good level of knowledge of the placement sites to start to develop a reasonable understanding of hyrax behaviour.
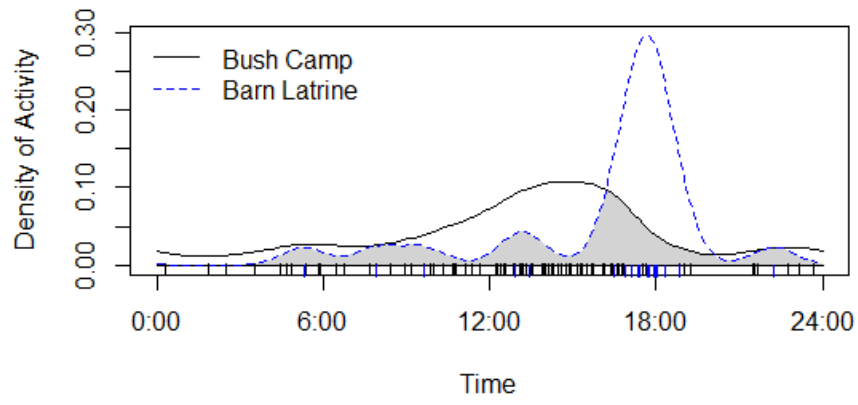
Figure 4.12: Density of hyrax activity across the 24-hour period at latrine sites, Bush Camp and Barn (see Figure 2.12 for exact location within field site). The short vertical lines at the bottom of the plot indicate the times of day at which the species were photographed.

Discussion

This chapter aimed to examine the diurnal behavioural profile of hyrax in relation to previous findings and subsequently to disentangle the relationship between an animal and its habitat as well as the proximate factors that could alter that relationship. These factors could be a restrictive force or indeed allow the animal greater freedom to utilise the variation within their habitat to the fullest extent.

Seasonal activity

It is clear from the results of the Overlap analysis (Figure 4.2) that there are obvious changes in the activity pattern of hyrax living in the Soutpansberg Mountains when there is a shift in temperature. The most striking of these activity profiles occurs in winter where the activity reflects a typical diurnal activity pattern (Figure 4.4: Winter).

By examining the density of activity for hyrax between sunrise and sunset throughout the year it became clear that spring, summer and autumn had similar unimodal activity profiles to the exclusion of winter which appears bimodal. Both of these activity patterns are recognised within the literature with varying explanations as to the cause and the benefits of each pattern. Coe (1962) observed rock hyrax on Mount Kenya and demonstrated that at high altitudes rock hyrax are more restricted in their ecology than lowland species and show a strong relationship between sunlight and activity but that the driving force behind the activity profile is food availability, as it is limited by the altitude. In a lower altitude habitat, the Mountain Zebra National Park in the Eastern Cape of South Africa, Fourie et al. (1987) showed, from field observations, that hyrax in the area foraged for between 0.5 and 8 hours at any one time and found no evidence of a bimodal activity profile. In contrast Sale (1965a) observed hyrax in the Serengeti, Kenya and in a captive environment and presents findings of a bimodal activity profile in the Serengeti only. This indicates that hyrax can be flexible in their activity profile depending on the energetic demands of the surrounding habitat. It is widely reported that hyrax cannot completely control their internal body temperature (Brown and Downs, 2006; Downs et al., 2013; Taylor and Sale, 1969) which may help to explain the results. Confirmed by general linear models showing significant relationships between temperature and density of activity for all four seasons, this finding is supported by Sale (1970) who describes hyrax needing to use behavioural thermoregulation such as basking and huddling together to exploit solar radiation and preserve heat by contact with conspecifics.

Conversely when the relationship between rainfall and density of activity of hyrax between seasons was investigated there was a complete absence of a relationship. Rainfall may have no seasonal effect on behaviour for a number of reasons but primarily because there is no clear profile in terms

of time of rainfall in the region therefore it cannot have a consistent effect (Figure 2.6). It was shown here that hyrax avoid any form of activity when it is raining but if it does not rain they behave normally. Additionally hyrax, especially rock hyrax, have a highly efficient grazing method that enables them to fill their stomachs in a short space of time allowing them to forage when the conditions are optimal and avoid the sporadic rainfall that occurs within the Soutpansberg Mountains (Sale, 1965a; Sale, 1966a). Moreover, both rock and bush hyrax choose to shelter in rock crevices due to the rocks insulating properties which maintains a more stable environment within the crevices allowing hyrax to shelter during rain events and preserve energy which they can then expend on foraging after the rain event (Olds and Shoshani, 1982; Sale, 1966b).

Behavioural activity

To understand the behavioural composition of hyrax activity profiles in a broader context, the images from the hyrax cameras were analysed for their behavioural content. These behavioural data revealed three core behaviours: travelling, resting and basking, and that these behaviours showed very different profiles.

Travelling is the main behaviour exhibited during the dark hours of the 24-hour cycle, which is surprising given that hyrax are a key prey species for primarily nocturnal mammalian predators within the Soutpansberg Mountains (Berger et al., 2003; Chase-Grey, 2011a; Fitzgerald, 2015b; Schwarz and Fischer, 2006; Stuart and Stuart, 1993) (see Chapter 3). It could be the case that if activity is necessary during this dangerous period, i.e. visiting a latrine, then it is efficiently executed to minimise risk and, therefore, the levels of travelling behaviour captured on camera traps may be biased by the activity of the nocturnal phase.

Basking can only occur in daylight hours. However, in the winter months, when data from the hyrax camera array were collected, it appears to be further restricted as it began at 06:30 in line with the average time of sunrise but ceases at 16:30, an hour earlier than the average time of sunset during the winter months. This may be due to the hyrax reacting to a steeper decline in temperature around sunset in the winter months and choosing to stop basking earlier in order to seek shelter or to commence foraging during the last hour of daylight. Basking is also positively correlated with minimum overnight temperature demonstrating the severe effect that low overnight temperatures can have on the physiology of hyrax and thus the activity profile of the following day. When modelled both rainfall and average temperature approached significance, however, site as a random effect accounted for 23.3% of the variation. These results indicate that this relationship requires further investigation; an approach to this could be collecting and analysing behavioural

and environmental data at a finer scale at a greater number of sites and producing larger sample sizes at each site.

Resting behaviour showed a more variable profile than either basking or travelling. This could indicate that hyrax alternate between resting and basking in order to maintain their internal body temperature within their thermoneutral zone. In contrast to the seasonal result, the more immediate effect of rainfall was examined and it had an entirely different effect on activity. When rainfall and activity were analysed on a daily scale, activity levels dropped significantly on days when rainfall occurred indicating that hyrax appear to not leave their sleeping sites within koppies when it is raining, most likely because the energetic losses incurred by getting wet and cold are greater than the energetic losses of a missed foraging opportunity (Fourie et al., 1987). Furthermore, when resting behaviour is modelled, rainfall is the only factor that approaches significance indicating that when hyraxes are caught out of their shelter during a rain event they are most likely resting. This result calls for further testing of this hypothesis with additional studies on resting behaviour in hyrax.

There are caveats attached to the behavioural activity analysis and both centre on the reliability of the camera traps to capture activity. Firstly, behaviour detected on camera traps can only be divided into very general behaviours and may not always be easy to determine in a static picture, particularly for species where little is known about their behaviour. Sampling can also be biased to specific locations influencing the behaviour(s) captured as demonstrated in the site specific analysis in this study. Likewise, cameras in certain locations may have very low picture frequency and capture little behaviour making systematic sampling difficult. Secondly, with the technological advances in this field of ecology the success of camera traps operating under adverse weather conditions such as extreme precipitation and temperatures is increasing (Swann et al., 2011) and with this being the first attempt to use camera traps to study hyrax in this area it is difficult to measure the impact that weather and other environmental conditions had on the image capture rate. It is unlikely to be a negative effect as indicated by anecdotal evidence (images recorded during rain events). Moreover, the cameras are light triggered passive cameras which use a beam of infrared light to detect changes in temperature within the field of view of the camera, complemented by a second sensor that detects changes in light levels (Swann et al., 2004). This type of camera is specifically recommended for the conditions experienced in the Soutpansberg Mountains as they have been shown to work efficiently during adverse weather conditions including rain. This is because rain will reduce the ambient air temperature therefore increasing the temperature gradient between the air and the target animal, therefore increasing the sensitivity of the infrared sensor and maximising the cameras ability to detect its target (Swann et al., 2011).

Site specific activity

By grouping the camera trap stations into habitat type the relationship between certain ecological characteristics and the presence of hyrax was explored. Furthermore, the way hyraxes utilise these habitat types when undertaking their daily activities could shed light on daily activity profiles and behavioural traits of hyrax within mountainous environments like the Soutpansberg region.

The comparison of activity profiles from PPP station 18a and Louisville demonstrated that hyrax show consistency over time in the way they use a site. This result could contribute to an explanation of why relocation and repopulation efforts with hyrax have failed (Wimberger et al., 2009), as males are territorial and can have a lifespan of up to 12 years in the wild (Olds and Shoshani, 1982) so it is likely that the colony resident at the Louisville location is the same one captured by PPP station 18a. If hyraxes do not react well to being relocated and their behaviour profile changes they may become more vulnerable to predation in this new location (Coe, 1962; Demartsev et al., 2014; Hoeck, 1989; Wimberger et al., 2009).

By visualising the differences between the two sets of camera trap images used in this study an understanding of how hyrax utilise the terrain may be established. A key finding is that hyrax consistently utilise roads and game trails around their territory with the level of activity building throughout daylight hours in this habitat type delivering a unimodal activity profile. The use of roads and trails appears at first glance to be a risky behaviour as it has been shown that many predators also favour roads and trails when moving around their territory (Benítez-López et al., 2010; Davis et al., 2010; Dickson et al., 2005; Martins and Harris, 2013; Whittington et al., 2005). However, as the majority of the mammalian predators within the Soutpansberg Mountains demonstrate a mainly nocturnal activity pattern and hyrax a diurnal pattern there is less risk using roads and trails during the day than at night. However, as Benítez-López et al. (2010) showed that raptors show a preference for hunting above roads and are an obligate diurnal species, due to the need for thermal drafts required for flight, they could potentially pose the highest risk to hyrax during the daylight hours. The activity profile seen when focusing on the roadside habitat does support more intense activity and feeding sessions in the afternoon as described by Meltzer (1973) who observed rock hyrax in Syria foraging for three to four hours a day to achieve adequate food intake with the foraging becoming more intensive later in the day (Hoeck, 1975; Sale, 1965a; Sale, 1966a).

Cliff sites are typically used as sleeping sites by hyrax due to the high availability of crevices that are utilised as protected sites to shelter and sleep in overnight. The unimodal activity profile seen at cliff sites could indicate that hyrax come and go from shelter and their sleeping site in between activities throughout the day and return for the final time late afternoon causing the singular late afternoon peak. This may also be an artefact of the small home range of hyrax and the wide variety

of vegetation that they can consume, both of which result in hyrax not venturing great distances from their central place (Druce et al., 2006; Hoeck, 1975; Hoeck, 1982; Kotler et al., 1999; Sale, 1965a; Sale, 1965c). Moreover, the activity profiles from the two woodland habitats most closely resemble a bimodal foraging activity pattern which is most likely the habitat type hyrax travel to from the cliff sites. An early spike in activity, foraging begins, followed by a drop in activity during the hottest part of the day concluding with a small spike in activity, afternoon foraging activity and returning to sheltered sleeping sites (Druce et al., 2006; Kotler et al., 1999). The sites where basking took place have the most consistent levels of activity which could be due to hyrax being a very inactive mammal and favouring resting and basking to limit the energetic output and save energy for the short but intensive bouts of feeding that occur early in the morning and late in the afternoon (Sale, 1965a; Sale, 1966a, b). The two basking sites were located in a koppie that supported a small population of hyrax so the continual activity shows that individual activity was constant across this time period and could suggest that this colony did not necessarily forage or travel as a group.

The two latrine sites were monitored for different periods of time. The difference in active days could account for some of the variation in activity profiles at these latrine sites. The defined spike in activity at 18:00 is an interesting result; whether it has any behavioural or ecological significance is yet to be determined as the formation of latrines by hyrax species is well established however the activity profile surrounding their use is not (Shoshani, 1992).

The estimation of overlap between the two Barn sites shows that the sites were used at different times of the day. When the images are examined it is clear that these two sites were used for different purposes. The Barn Fence site is in direct sunlight for a large part of the day and is, therefore, used by the hyrax for behavioural thermoregulation (basking). The Barn Latrine site which is located on top of a boulder covered by a fig tree and is the site of a hyrax latrine. This analysis neatly summarises many elements of hyrax behaviour by showing that they differentiate sites based on ecological requirements on a small scale as well as the large scale site specific behavioural examples described above.

Conclusion and Future directions

There are four main conclusions from this study:

1. The general activity profiles of the four seasons showed that spring, summer and autumn are similar with the exclusion of winter which is bimodal while spring, summer and autumn profiles all show a largely unimodal pattern.

2. Temperature has a significant effect on seasonal density of activity of hyrax with low minimum overnight temperature increasing the level of basking behaviour the following day.

3. Rainfall has no effect on seasonal density of activity but does cause a cessation in activity outside of the koppie habitat so is still an important ecological constraint.

4. Hyrax clearly utilise different sites within their habitat as shown by definitive site specific behaviours such as basking.

5. Preliminary results indicate hyrax activity profiles remain consistent over time.

This chapter and the questions it addresses were born from the disjunct nature of the two sets of images collected during the fieldwork in South Africa. It has shown that there are implications for camera trapping as a method for studying certain animals and certain behaviours, especially central place foragers for whom the area covered during daily activities may be small. In this case the placement of camera traps must be carefully considered in order to adequately capture behavioural data at the same time limiting repeat captures that may cause interference during the process of analysing the data and forming robust conclusions based on the results. As this study evolved, camera trapping which was initially a method of quantifying interference in the primary experimental method of giving-up density experiments became the principle method for examining hyrax behaviour in the Soutpansberg Mountains. The results of this study only give a brief outline of the types of analyses that could be conducted on hyrax and other small mammals within mountainous habitats using camera traps and it also highlights issues with this methodology and hopefully future studies of this kind can learn from this methodology and improve the use of camera traps in studying small mammals and specifically central place foragers.

Chapter 5 : Discussion and Conclusion

Summary

Rock and bush hyraxes are small mammals native to the African continent that have been understudied despite their significance as a prey species within many predators' diets. The aim of this study was to investigate the spatial and temporal activity of these two species within the forest habitat of the Soutpansberg Mountains in northern South Africa. Initial plans to examine the landscape of fear in hyrax based on giving up densities did not work out since the animals did not utilise the experimental trays. As a consequence, the thesis instead drew on an extensive database of camera trap images to explore key facets of hyrax behaviour.

Chapter 3: Sleep wake cycle of hyrax

When observed throughout the 24-hour period there is supporting evidence that hyraxes have the potential for a flexible sleep wake cycle as shown by the low but consistent level of nocturnal activity detected by two camera trap arrays placed across the Soutpansberg Mountains. No evidence was found for ecological factors promoting nocturnal behaviour. Contrary to expectations, the effect of day length was an increase in nocturnal activity during the summer months when nights were shorter which is likely due to the higher average overnight temperature allowing the hyrax to remain active for longer. In winter the shorter days and lower overnight temperatures means there is a high energetic cost to activity at this time as they cannot maintain their body temperature in opposition to the cold. Lunar phase had no effect on hyrax activity despite the full moon phase offering increased light levels for foraging and predator detection. Ultimately nocturnal activity in hyrax appears constrained by the high levels of predator activity during the dark hours within the Soutpansberg Mountains. A lack of variability in predator activity across the lunar cycle suggests that predation is a relatively constant pressure meaning that the risk of predation has a greater effect than the benefits available to hyrax were they to remain active after dark on moonlit nights.

Chapter 4: Activity patterns of hyrax in a mountainous environment

It is clear that hyrax, due to their physiological limitations such as inadequate endothermic thermoregulation, show the potential to adjust to seasonal changes in temperature throughout the year, however, there was no indication that rainfall had any impact on their temporal activity

when viewed on a seasonal basis; this may be due in part to the erratic nature of rainfall in the Soutpansberg Mountains. Nevertheless, on a daily basis rainfall had a significant impact of activity levels, with few hyrax visible on days with rainfall. Hyrax may only utilise a small part of the landscape, however, it is clear from the results of this study that they exploit very specific characteristics of the habitat to maximise their energetic gains and reduce their energetic loses. In particular, basking or behavioural thermoregulation using solar energy, is a well documented behaviour in hyrax (Sale, 1970) and has been shown in this study to occupy a large part of the diurnal activity profile of hyrax in the Soutpansberg Mountains. Furthermore, basking increases after cold nights, highlighting its importance as a thermoregulatory mechanism. While camera traps have limitations for studying small mammals they can nevertheless provide valuable insights into patterns of behaviour.

Studies of hyrax landscapes of fear – constraints and opportunities

Studying predation risk in hyrax within a forest environment was challenging. A better understanding of basic hyrax ecology in an environment like the Soutpansberg Mountains is required before the more specific questions relating to predation risk can be investigated.

The initial method of giving-up density experiments employed to study hyrax failed due to interference from primate species and no interaction by hyrax with the trays or food trials (Chapter 2). This is not to say that GUDs would not be successful in the Soutpansberg Mountains, since they have been employed in other mountainous locations (Bedoya-Perez et al., 2013; Druce et al., 2009), but pilot studies where foods and locations are trialled in combination with each other may lead to a better knowledge of the components of the GUD protocol, which need to be adjusted for hyrax. It may be the case that changing the location of the GUDs by moving away from locations where primates are habituated and been exposed to GUD experiments within the Soutpansberg Mountains may limit or even remove the interference from allospecifics. A more extensive food trial protocol may deliver a food source that is both adequate for the GUDs and attractive to the target species. Finally, trialling different apparatus in the form of trays and buckets to facilitate easy access for hyrax and encourage interaction with the GUDs.

Due to the GUD experiments being unsuccessful this lead to camera trapping taking over as the primary investigative tool for answering questions about hyrax behaviour in the Soutpansberg Mountains. Camera trapping has been used in a wide variety of contexts (Bridges and Noss, 2011; Kucera and Barrett, 2011; O'Connell et al., 2011; Silver et al., 2004; Tobler et al., 2008), as well as within the study area (Baker, 1938; Chase-Grey et al., 2013; Fitzgerald, 2015b), although cameras

are less frequently used for smaller species (De Bondi et al., 2010). Nevertheless, cameras proved to be a successful way of monitoring activity patterns and capturing certain behaviours in hyrax, although for future studies the experimental design requires refinement. Detailed information about camera position such as aspect and elevation, if standardised, would have aided in making robust conclusions about habitat use by hyrax. The implementation of a new camera trapping protocol and the use of two different sets of camera traps resulted in highly variable data, especially in terms of the behaviours captured, which limited the analysis that could be conducted and, therefore, the questions that could be posed about hyrax and their activity patterns and behaviour. The camera traps that were installed to monitor hyrax colonies were not laid out in a structured way due to the location of confirmed hyrax colonies within the study site. To substantiate the results presented here the hyrax population in the Soutpansberg Mountains require a more regimented camera trapping protocol additionally locating and incorporating a greater number of hyrax colonies would give the analysis more power and enable robust conclusions to be made. Furthermore, the results clearly highlighted that the location of the camera (e.g. basking site vs. latrine site) could significantly influence the number and temporal pattern of images obtained. As a consequence, any future camera-trapping protocol may also need to conduct a series of habitat assessments at each location to determine the key environmental features associated with each location.

The parameters used to design camera trap arrays are as varied as the species captured by them and there is no consensus on the optimal design of camera trap arrays (McCallum 2012). Kays et al. (2009) emphasises the relationship between increased sample size and increased statistical power. The conundrum of how to maximise sample size is a juggling act between improving the likelihood of detecting a species at a given site because longer runs are better; increasing the number of different sample units that can be surveyed during the field season as shorter runs result in greater number of sites being surveyed; and, for more specific questions, maintaining population closure at a site, no immigration or emigration, may be important (Kays et al. 2009). Given this dilemma Keys et al. (2009) compared and contrasted a camera array on trails and a randomised camera array across the whole site. Only three out of the 14 species came out as having significantly different capture rates from the two arrays. Ocelot was six times more likely to be captured by a trailside camera but brocket deer (*Mazama* spp.) and peccary (Family: Tayassuidae) avoid trails with 2.8 and 3.3 times more images of these species captured on cameras placed in the forest and the other 11 species showed little to no difference. The conclusion from this data and the consensus from the literature in general is that of matching the design of the camera array to the question(s) and therefore the data that is best suited to answering the question(s) (Rowcliffe et al., 2008a). Grid patterns generally don't work for carnivores (O'Connell et al. 2011) or small mammals (Rowcliffe et al., 2008b) but semi-structured

stratified random arrays in high quality habitat were shown to be successful at capturing grizzly bears (Kucera and Barrett, 2011). If the objective is for an overall survey of the fauna of an area, then a grid system can and has been used successfully (Rowcliffe et al., 2008b). The pitfalls of this method including biased capture rate for small or large animals depending on the height of the camera, must be taken into consideration (Rowcliffe et al., 2008b).

Furthermore, it would be advantageous to attempt to estimate population densities for the two species of hyrax that inhabit the Soutpansberg Mountains and ascertain the species composition of colonies which would allow for comparative studies to be conducted as has already been done in other parts of their range (Barry, 1994; Barry and Mundy, 1998; Barry and Mundy, 2002).

Future Directions

There is considerable scope for future studies on all aspects of hyrax ecology. From this study, it is clear that further studies are needed on hyrax living in predator free environments such as zoological collections and in-situ predator free landscapes to test if those animals are more flexible in their sleep wake cycle and show higher levels of nocturnal activity as the laboratory based studies suggest. There have been unsuccessful attempts to reintroduce both captive and wild hyraxes into suitable habitat which have failed due to all hyrax succumbing to predation which could be contributed to the activity patterns of hyrax and their predators coinciding (Wimberger et al., 2009). This highlights the importance of pre-release training in reintroductions (Beck et al., 1994), but current protocols are unlikely to consider the need to 'train' changes in activity phase before the animals are released.

GUD experiments are a proven method for studying the landscape of fear in hyrax (Druce et al., 2006; Kotler et al., 1999). However, a full assessment resulting in a clear understanding of the potential study site is required to limit the risks of interference from non-focal species. Furthermore, preliminary work such as trialling multiple food types to determine the most appropriate food for the species and the area to maximise visitation rates of the target species. Despite the unsuccessful implementation of GUDs for this study it could be useful to pursue this type of experiment in the Soutpansberg Mountains. Classic GUD experimental design is covered versus uncovered trays when placed in the context of raptor behaviour would give the best understanding of level of exposure hyrax incur from raptors. Possible solutions for successful GUDs could include more comprehensive and longer lasting food trials to determine if hyrax would consume a processed food such as feed pellets or if an alternative is required. This alternative could be a form of dried foliage or grass as hyraxes are known to consume low quality vegetation during the winter months and if it is pre-dried then the weight of the food, which is a

crucial factor in GUD methodology, should remain consistent throughout the experimental period. Irrespective of the design it is clear that hyrax, with their slow life history but high levels of apparent predation are an important study system for addressing questions about the importance of predation risk.

An addition to the camera trapping protocol could be the implementation of telemetry including GPS telemetry, VHF or radio telemetry and accelerometers. Radio telemetry is currently being used to monitor both the brown hyaena and leopard populations in the Soutpansberg Mountains (Williams, *submitted*; Williams et al., *in review*) but has not been used on the small mammals found in the region. Using telemetry alongside camera traps is now common place in the study of activity patterns of carnivores. For example, Maffei et al., (2005) conducted an initial camera trap survey of ocelot activity patterns but in concluding the findings alludes to an additional study using radio telemetry that will be used to confirm the preliminary camera trap data and give an independent density estimation for the ocelots in that region. Using these two technologies in tandem can emphasise flaws in one or both of the methods. Soisalo and Cavalcanti (2006), the first jaguar population estimate using camera traps conducted in cooperation with GPS telemetry compared the density estimations from both methods over two seasons. It was clear that the estimates from the GPS telemetry (6.6 individuals/km^2 and 6.7 individuals/km^2) was consistently and significantly smaller and more accurate than those constructed using mean maximum distance moved (MMDM) from the camera trap data (10.3 individuals/km^2 and 11.7 individuals/km^2). The experimental designs can also bias the results, especially when looking at the placement of camera traps. Te Wong et al., (2004) used radio telemetry and camera traps to study sun bear (*Helarctos malayanus*) activity patterns with vastly different results. Camera traps produced a crepuscular, nocturnal activity pattern contrasted with the strictly diurnal activity pattern of continuous activity from sunrise to sunset seen in the radio telemetry data. This was attributed to the biased placement of the camera traps by trails, water sources, mud wallows, trap sites and the presents of bait. If used correctly these two technologies can be very complementary and can build a comprehensive picture of the activity patterns of the focal species. Luechtenberg et al., (2014) chose to use both technologies to study the activity pattern of giant river otters (*Pteronura brasiliensis*) but they chose to only actively monitor one technology at a time with the radio telemetry active from 05:00 until 19:00 and the camera traps placed at denning sites to capture nocturnal activity. The radio telemetry showed giant river otters were crepuscular and diurnal but 31% of camera trap data was nocturnal. Peaks in activity at the dens occurred at 06:00 and again between 16:00 – 19:00 with nocturnal activity at the den dominated by defecation, opportunistic hunting and disturbance by predators. These studies exemplify the complex nature of studying animal activity patterns and that both telemetry and camera traps have benefits and problems. Telemetry gives access to more animal specific information including

age, sex and reproductive status but can also be biased due to the trapping and handling protocol required to fit the device (O'Connell 2011). Camera trapping can overcome some of these issues but can deliver equally biased data if the placement of the cameras is not optimal for the target species and the questions posed (Dillon and Kelly 2008).

Conclusions

This study represents the first of its kind on hyrax in the Soutpansberg Mountains and has shown novel behaviour in wild hyrax by demonstrating the presence of nocturnal activity. This information could be looked upon as pilot information for future studies on hyrax within mountainous forest habitats and beyond with a view to further testing the hypothesis that hyrax have a flexible sleep wake pattern and are not fundamentally diurnal.

Overall this study has shown that there is still a lot to learn about hyrax and their behavioural ecology. A better understanding of the behavioural ecology of these species could have practical implication for conserving threatened species for which hyrax are a key prey item including leopards, black eagle and crowned eagle.

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