

# **Eavesdropping: How do vervet monkeys perceive the alarm calls of other species?**

by

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## ABSTRACT

Perceived predation risk has a large impact on how prey species utilise landscapes. In an effort to reduce predation risk, individuals tend to utilise safer areas more than unsafe areas. How perceived predation risk affects the utilisation of landscapes by animals is termed a “landscape of fear”. Vervet monkeys (*Chlorocebus pygerythrus*) have a landscape of fear that operates in both horizontal and vertical planes. Within this landscape, vervets perceive the safest area to be up in a tree, under the canopy. To reduce predation risk, vervets use various predator-specific alarm calls and have been found to eavesdrop on the alarm calls of other species (e.g. birds). In this study, I explored whether vervet monkeys were able to associate eavesdropped alarm calls with specific predator types (i.e. aerial and terrestrial) as they do with their own predator specific alarm calls. To do this, I first quantified the three-dimensional landscape of fear for vervet monkeys by measuring giving up densities in artificial patches. I then used playbacks of the vervets’ aerial and terrestrial predator alarm calls, the alarm call of a red-backed shrike, and a mixed-species flock mobbing call to manipulate perceived predation risk. By comparing changes in foraging intensity within the patches, I quantified the specific reactions of the vervet monkeys to aerial and terrestrial predators. In addition, I found that the monkeys did not eavesdrop on the red-backed shrike call. However, the vervets did eavesdrop on bird mobbing calls, and associated the calls with the location of the potential treat and reacted as if it was a particular predator type. Specifically, the vervets reacted to mobbing calls played from up in a tree the same way as they did if an aerial predator was present, and calls from the ground as if a terrestrial predator was present. Thus, this suggests that they were able to associate a non-functional referential call (i.e. the mobbing call) with specific information, gathered from the location of the calls, and interpreted it in a referential manner. Moreover, intensity of these reactions (as measured by total feeding effort) indicated that vervets saw aerial predators as a greater threat compared to terrestrial predators. Ultimately, my results suggest that vervets can associate eavesdropped calls with specific predators, and this likely provides a fitness benefit in a dangerous and unpredictable world.

## DECLARATION

The work described in this dissertation was carried out in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Dr. Adrian M. Shrader and co-supervised by Mr. Hallam Payne. This work took place between February 2012 and November 2013.

I declare that the work submitted within this thesis is my own work. This work is submitted for the fulfilment of a Master in Science in Zoology at the University of KwaZulu-Natal.

This full work, or partial sections, has not been submitted for any other degree or examination at this university or any other tertiary institution.

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## CHAPTER 1: INTRODUCTION

### 1.1 Communication

Animal communication is the proximate cause of a wide range of animal behaviours (Alcock 1998). Essentially, it is the transfer of information from one individual to one or more individuals (Halliday and Slater 1983; Alcock 1998). This transfer can comprise a range of information, such as mate recognition, territorial awareness, and day-to-day social information transfer (Breed and Moore 2012). Non-random signals are used to convey specific messages, and are intended for a specific receiver by a specific sender (Maynard Smith 1965; Breed and Moore 2012). Signals are sent in many forms, including colour, actions, chemical compounds or electromagnetic outputs (Halliday and Slater 1983; Breed and Moore 2012). Auditory communication is one of the most commonly recognised forms of information transfer, and can be a highly effective tool in transmitting knowledge (Breed and Moore 2012). Alarm calling is one such example.

### 1.2 Alarm Calling

Alarm calling is a means to communicate the presence of a predator to either con- or hetero-specifics (Maynard Smith 1965). Sciurids (Digweed and Rendall 2009; Giberson 2011), primates (Cheney and Seyfarth 1980b; Zuberbühler *et al.* 1999a; Fichtel and Kappeler 2002) and passerine birds (Marler 2005) are well known for their alarm calling behaviour. The information transmitted varies according to species, and can include type of threat, direction and urgency. For example, functionally referential alarm calls found in a range of primates (E.g. Seyfarth *et al.* 1980a; Zuberbühler 2000b; Zuberbühler 2001; Arnold and Zuberbühler 2006) and sciurids (E.g. Sherman 1985) can indicate the type of threat, most commonly categorized into aerial or terrestrial predators. Mobbing calls given by groups of birds can also be a reliable indication of the direction of a predator (Curio *et al.* 1978; Johnson *et al.* 2003). Additionally, other species such as redfronted lemurs (*Eulemur fulvus rufus*), white sifakas (*Propithecus*



*verreauxi verreauxi*) (Fichtel and Kappeler 2002) and California ground squirrels (*Spermophilus beecheyi*) (Leger and Owings 1978; Leger *et al.* 1979) can indicate degrees of urgency by using acoustically distinct alarm calls.

There are several theories concerning the evolution of alarm calling behaviour. The production of an alarm call to warn conspecifics seems an example of altruistic behaviour (Maynard Smith 1965; Sherman 1977; Hollén and Radford 2009). An individual calling may attract attention to themselves and increase their vulnerability to attack (Maynard Smith 1965; Hollén and Radford 2009). Kin selection, first hypothesised by Hamilton (1964), explains how this may have evolved, in that an individual acting to warn close relatives of an impending threat increases the chances of passing on their genes indirectly through the success of their kin.

There are many other hypotheses that are also used to explain the evolution of alarm calls. The predator deterrence hypothesis suggests that alarm calls are directed at predators in an effort to drive them off (Woodland *et al.* 1980; Cresswell 1994; Zuberbühler *et al.* 1999a). For example when threatened by a predator, the eastern swampphen (*Porphyrio porphyrio*) flicks its tail, in an attempt to communicate to the predator it has been identified, and further pursuit of the hunt is futile (Woodland *et al.* 1980). Woodland *et al.* (1980) noted this behaviour in both solitary birds and those in groups, indicating that this communication is directed primarily at the predator. Similarly, Zuberbühler *et al.* (1999a) found that in the Taï forest of Côte d'Ivoire, Diana monkeys (*Cercopithecus diana*) gave loud conspicuous alarms when sighting leopards (*Panthera pardus*), yet soft inconspicuous alarms when sighting chimpanzees (*Pan troglodytes*). When making alarm calls in response to the presence of a leopard, the Diana monkeys were directing the alarm at the leopard, which then gave up its hiding place and abandoned the hunt. However, when making alarm calls for a chimpanzee, the alarms were directed at conspecifics - chimpanzees were not deterred by alarms, as they chase down their prey rather than relying on the element of surprise (Zuberbühler *et al.* 1999a).

Another hypothesis to explain the evolution of alarm calling is that alarm calls benefit the caller by manipulating conspecific (or even heterospecific) behaviour to benefit oneself (Sherman 1977). An example of this can be found in Belding's ground

squirrels (*Uroditellus beldingi*) (Sherman 1985). These squirrels alarm call for both aerial and terrestrial predators. Sherman (1985) found that the most vulnerable individuals (i.e. those far away from cover and conspecifics) were the ones that made alarm calls most for aerial predators. Once an alarm was called, conspecifics retreated to cover, causing a brief moment of pandemonium on the ground. Sherman (1985) hypothesised that this confused predators, and provided an opportunity for the original caller to escape predation.

Mobbing is another example of how individuals can manipulate conspecifics to gain an advantage. Wheeler (2008) found that the mobbing calls given for model felids by capuchin monkeys (*Cebus apella nigratus*) were directed at both the model predator and to conspecifics. The initial caller started the mobbing, and was joined by other conspecifics. Therefore, with strength in numbers they are able to drive predators away (Wheeler 2008). As seen in this example, these alarm call theories are not mutually exclusive, as both predator deterrence, and conspecific manipulation can be supported by the behaviour of capuchin monkeys.

Alarm call types may be categorized into two broad groups: flee alarms and mobbing calls (Leavesley and Magrath 2005). Flee alarm calls are further broken down into affective flee calls and specialized alarm calls. Specialized calls are then divided into urgency-based signalling, and functionally referential calls (“response urgency” and “referential signalling” *sensu* (Macedonia 1990)). Affective flee calls are a simple alert of a predator, without any information regarding the degree or the type of threat (Leavesley and Magrath 2005). For instance, ruffed lemurs (*Varecia variegata*) have an alarm call that only indicates the presence of a predator, and is primarily based on the emotional or motivational state of the caller (Macedonia 1990).

Unlike affective flee calls, specialized calls (i.e. urgency and functionally referential calls) provide additional information about a recognised threat (Furrer and Manser 2009). Urgency alarm calling provides information to the receiver about the degree of urgency of a threat, and is found in passerine birds (Klump and Curio 1983; Naguib *et al.* 1999), sciurids (Leger and Owings 1978), murids (Le Roux *et al.* 2001) and primates (Fichtel and Kappeler 2002). These calls vary in volume (Leger *et al.*

1979; Ficken 1990), acoustic structure (Klump and Curio 1983; Fichtel and Kappeler 2002), composition (Nagiub *et al.* 1999) and repetition (Leavesley and Magrath 2005).

Among passerines, willow tits (*Pardus montanus*) lengthen their alarm calls when risk is increased (Haftorn 1993), and Mexican chickadees (*Parus sclateri*) increase the pitch of their alarm calls with increasing predator threats (Ficken 1990). White-browed scrubwrens (*Sericornis frontalis*) also use an urgency-based alarm system. They have a single trill alarm call to which they add more elements in proportion to the degree of predatory threat (Leavesley and Magrath 2005). As a result receivers were more likely to flee when there were more elements in the alarm call (Leavesley and Magrath 2005).

In sciurid and murid rodents, California ground squirrels give two distinct types of alarm call to the same predator, depending on how far away the predator is from the caller. Ultimately, this transmits information regarding the degree of urgency (Leger and Owings 1978; Leger *et al.* 1979). Olympic marmots (*Marmota olympus*) vary the number and rate of their alarm calls in relation to predation risk, while Vancouver Island marmots (*Marmota vancouverensis*) encode risk by varying the duration and composition of their calls (Blumstein 1999a). Brants' whistling rats (*Parotomys brantsii*) also use an urgency-based system of short- and long-duration alarm calls that transmit a perceived level of threat, but not the type of predator (Le Roux *et al.* 2001).

Among primates, Fichtel and Kappeler (2002) found that redfronted lemurs and white sifakas have a mixed alarm call system. They have predator-specific calling for raptors, and non-specific urgency-based alarm calling for terrestrial predators (Fichtel and Kappeler 2002). Urgency-based alarm calling provides enough information to warn conspecifics of a potential threat, and to give them an indication of a degree of that threat. However, in some species simply a warning of urgency is not sufficient, as prey animals needed to know the type of threat in order to respond to predation risks effectively.

Functionally referential alarm calling allows prey animals to pass on specific information about predator types using only their alarm calls (Fichtel and Kappeler 2002; Gill and Bierema 2012). In order to be classified as functionally referential, the alarm call needs to be predator-specific, and context-independent (Blumstein 1999b;

Gill and Bierema 2012). Functionally referential alarm calls evolved through the need to know the specific predator in order to perform the correct escape response (Cheney and Seyfarth 1990; Evans *et al.* 1993). Prey animals that are hunted by several predators with different hunting strategies need to know what predator is hunting them in order to escape effectively (Blumstein 1999b). This is especially important when the escape from one predator could lead straight into another, which is likely in complex habitats (Macedonia 1990). For example, several different predators using different hunting strategies hunt ring-tailed lemurs (*Lemur catta*) in the complex forested habitat in which they live (Macedonia and Evans 1993). As a result, the lemurs have developed different escape responses for each predator, and information regarding predator type is essential, particularly in such a variable habitat (Macedonia and Evans 1993).

Urgency-based alarm calls are therefore most commonly found when prey live in uniform habitats and only have one escape strategy, such as retreating into a burrow, while functionally referential calling is found when there are several predators in a more complex environment (Furrer and Manser 2009). For this reason functionally referential alarm calls are most commonly found in primates (Seyfarth *et al.* 1980b; Macedonia 1990; Zuberbühler 2001; Seiler *et al.* 2013). However, some species of small ground-dwelling mammals, such as meerkats (*Suricata suricatta*) (Manser 2001) and Gunnison's prairie dogs (*Cynomys gunnisoni*) (Slobodchikoff 1991; Placer and Slobodchikoff 2000), as well as one species of bird, the red jungle fowl (*Gallus gallus*) (Collias and Collias 1967; Gyger *et al.* 1987) have also been found to use this form of specialised alarm calling. For instance, meerkats have acoustically distinct alarm calls which denote aerial and terrestrial predators, resulting in variable degrees of escape to their burrows (Manser 2001; Manser *et al.* 2001). Additionally, they have a third distinct call for group aggregation, which is called when snakes or deposits such as faecal matter or urine are found and need investigation (Manser *et al.* 2001). Among mammals, primates are the most well-known example of functionally referential alarm calling. Campbell's monkeys (*Cercopithecus campbelli*), Diana monkeys (Zuberbühler 2000a; Zuberbühler 2001) and vervet monkeys (*Chlorocebus pygerythrus*) (Seyfarth *et al.* 1980b) all have distinct escape strategies for aerial and terrestrial predators, triggered by acoustically distinct alarm calls.

A number of studies review the use of predator-specific alarm calls versus urgency-based alarm calls (e.g. Owings and Hennessy 1984; Macedonia 1990). Although prey species, such as California ground squirrels appear to give functionally referential alarm calls to raptors and terrestrial predators, this does not necessarily mean that these are in fact functionally referential (Owings and Hennessy 1984). Instead, these alarm calls could give an indication of time, and therefore urgency, of impending predation, as suggested by Gyger *et al.* (1987). The California ground squirrels response to raptors needs to be faster than to terrestrial predators, as raptors are an immediate threat, while terrestrial predators often are less immediate (Owings and Hennessy 1984). Hence, it seems that California ground squirrels refer to different predators in their alarm calls, as these alarms seem to be acoustically distinct. However, these are actually urgency calls that just happen to be commonly called in response to the same predators (Owings and Hennessy 1984). This is perhaps because ground squirrels only have one predator escape response for a variety of predators: retreat to the safety of their burrow (Fichtel and Kappeler 2002). Therefore, an urgency-based system is more useful than a functionally referential system for this species (Owings and Hennessy 1984).

This highlights one of the major challenges with assigning alarm call systems to specific species. Before any alarm system is assumed, intensive research is required to determine the finer details of alarm calling behaviour. It is therefore essential to tease apart how prey animals use their alarm calls, and specifically what they mean.

In contrast to flee calls, mobbing calls are acoustically similar in many species of related taxa (Johnson *et al.* 2003; Marler 2005). These calls are often broad-spectrum, loud and repetitive (Fallow *et al.* 2011). Prey species sound them when they spot a predator that is yet to be an immediate threat (Fallow *et al.* 2011). This often takes the form of a perched raptor, or terrestrial predator which has been spotted before attacking (Johnson *et al.* 2003; Lind *et al.* 2005). For example, when a snake is seen, meerkats sound their group aggregation alarm call, which causes the meerkats to group together and mob, or sometimes even kill, the trespassing snake (Manser *et al.* 2001).

Mobbing calls are intended towards both conspecifics and heterospecifics (Johnson *et al.* 2003; Marler 2005; Randler and Förschler 2011). They are designed to attract the attention of surrounding conspecifics and other similarly vulnerable species,

who then join in on the mobbing of the predator, and eventually drive it off (Randler and Förschler 2011). For example, Hurd (1996) found that 24 heterospecifics were attracted when black-capped chickadee (*Parus atricapillus*) mobbing calls were played in various playback experiments. This attraction results in mixed-species flock mobbing, which is likely essential for successful predator defence (Hurd 1996). In addition, mobbing calls alert predators that they have been spotted, which facilitates chasing them off (Randler and Förschler 2011). Moreover, mobbing provides safety in numbers (Randler and Förschler 2011). The system behind mobbing calls therefore allows conspecifics and heterospecifics to gather information regarding the location of potential threats (Lind *et al.* 2005). It is for this reason that mixed-species flocks successfully drive off a variety of predators through mobbing (Johnson *et al.* 2003).

There are, however, certain costs involved with alarm calling, whether these are flee alarms or mobbing calls. It has been hypothesised that calling increases the risk of predation to the caller (Hamilton 1964; Maynard Smith 1965). However many studies have attempted to quantify this, and several have found that there is no evidence of increased risk of predation to the caller (Sherman 1977; Cheney and Seyfarth 1985b). Additionally, it has been found that the cost of alarm calling is minimal compared to the potential cost of withholding a call. For example, the Arabian babbler (*Turdoides squamiceps*) alarm calls frequently, even in low risk situations, as the risk of not calling outweighs the benefits of withholding the call (Edelaar and Wright 2006). In conjunction with this, receiver animals should therefore respond readily to alarm calls, as the cost of ignoring a call could be potentially fatal. Therefore, in species in which alarm calls are used, the callers and receivers should be overly cautious, rather than underestimating a threat (Bouskila and Blumstein 1992; Edelaar and Wright 2006).

However, some individuals take advantage of this over-cautious approach. For example, the fork-tailed drongo (*Dicrurus adsimilis*) gives dishonest signals in the presence of pied babblers (*Turdoides bicolor*) in order to elicit a false response and benefit from heterospecifics reacting to the call (Ridley *et al.* 2007). Ridley *et al.* (2007) found that when pied babblers were foraging on the ground, a fork-tailed drongo would give a false alarm call. In turn, the pied babblers reacted to this call and fled to the safety of the trees. The drongo was then able to steal the food the babblers deserted.

However, this form of dishonest signalling only occurs with single individuals (Ridley *et al.* 2007). Mobbing calls are often a collaboration of many species, and thus dishonest signalling is unlikely to occur in such aggregations. It is for this reason that mobbing calls are considered to be honest and reliable signals indicating the presence of a threat (Lind *et al.* 2005).

### 1.3 Eavesdropping

Conspecifics sound alarm calls that are intended for specific receivers (Maynard Smith 1965; Breed and Moore 2012). These usually consist of close kin or related individuals. However, these are not the only individuals that may benefit from this alarm calling behaviour. When a vocalization is sounded, it enters the environment and becomes social information (Valone 1989; Fichtel and Manser 2010; Breed and Moore 2012). Both conspecifics and heterospecifics can take advantage of this information through eavesdropping (Fallow and Magrath 2010; Ito and Mori 2010; Breed and Moore 2012). Eavesdropping is the use of social information, intended for a specific receiver, that has been intercepted and used by heterospecifics (Cheney and Seyfarth 2005; Peake 2005). In many cases, the information is in the form of alarm calls. However other signals, including copulation, olfactory and behavioural signals, may be noticed and exploited (Peake 2005). In all cases however, the signal is non-random (Peake 2005). The signaller purposefully gave the signal, which was intended for a specific receiver, and intercepted by an eavesdropper (Peake 2005).

Not all species perceive the environment in the same way (Magrath *et al.* 2009). Therefore, eavesdropping may provide individuals with information that they are unable to acquire on their own (Magrath *et al.* 2009). For example, greater racket-tailed drongos (*Dicrurus paradiseus*) make detailed discriminations in their alarm calls for aerial threats, whereas orange-bellied babblers (*Turdoides rufescens*) alarm call for all fast-moving aerial objects (Goodale and Kotagama 2005). Hence, within mixed-species flocks a variety of species eavesdrop on the more detailed drongo alarm calls rather than the general, and potentially incorrect babbler calls.

Eavesdropping ultimately allows individuals to indirectly increase their vigilance without having to invest additional energy (Lea *et al.* 2008). Therefore, eavesdropping likely provides a fitness benefit, and is thus expected to evolve (Peake 2005; Magrath and Bennett 2012). This allows the eavesdropper to relax their vigilance and focus on other activities such as foraging or finding a mate (Fallow and Magrath 2010).

Ultimately, for eavesdropping to be effective, it requires that the caller and the eavesdropper to be sympatric and share the same predators (Magrath *et al.* 2007; Carrasco and Blumstein 2012). This often occurs amongst similar taxa, but is not restricted to this situation (Carrasco and Blumstein 2012). For example, eavesdropping can occur between and within groups of mammals and birds (Cheney and Seyfarth 1990; Zuberbühler 2000a). Moreover, eavesdropping can occur on both flee and mobbing calls (Goodale and Kotagama 2008; Fallow and Magrath 2010). For example, Diana and Campbell's monkeys eavesdrop off one another's functionally referential alarm calls to aerial and terrestrial predators (Zuberbühler 2001). In order to exploit this they are often found in mixed-species groupings (Zuberbühler 2001). Yellow-casqued hornbills (*Ceratogymna elata*) can distinguish between and respond to Diana monkey alarm calls (Rainey *et al.* 2004). Red squirrels (*Sciurus vulgaris*) respond to urgency alarm calls of Eurasian jays (*Garrulus glandarius*) (Randler 2006). Eastern chipmunks (*Tamias striatus*) react to mobbing calls of the eastern tufted titmouse (*Baeolophus bicolor*) (Schmidt *et al.* 2008). Each signaller-eavesdropper dyad is found in the same area and shares predators.

There are three possibilities when it comes to the development of eavesdropping behaviour. First, it could be facultative, and eavesdroppers could be cueing off similar acoustic properties of heterospecifics (Fallow and Magrath 2010). If one species alarm call sounds similar to another's, they may view a closely related species' alarm as a sign for the same danger. However, it is not necessary for there to be acoustic similarity among signals (Fallow *et al.* 2011). The second option is that eavesdropping could have evolved to be an innate response, as eavesdropping provides a fitness benefit (Magrath and Bennett 2012). Finally, eavesdropping behaviour may be an adaptive, learned behaviour. When alarm calls are sounded regularly, and accompanied by the presence of



a predator, the call will likely be associated with the predator, and the eavesdropping response is thus developed through associative learning (Rainey *et al.* 2004).

According to Fallow *et al.* (2011) anything can be learnt to be a signal. For example golden-mantled ground squirrels (*Spermophilus lateralis*) experimentally learned a novel sound that indicated a model predator, demonstrating that signals can be learned as an adaptive response (Fallow *et al.* 2011). Similarly, superb fairy-wrens (*Malurus cyaneus*) learned to eavesdrop on noisy miners (*Manorina melanocephala*) only once they had lived with the miners (Magrath and Bennett 2012). This is advantageous as it allows species to adapt to an ever-changing environment (Magrath and Bennett 2012).

The degree of response to conspecific alarm calls versus heterospecific alarm calls can vary depending on the species' concerned. The collared pika (*Ochotona collaris*), for example, responds to the alarm calls from both yellow-bellied marmots (*Marmota flaviventris*) and golden-mantled ground squirrels. However, collared pika have a greater response to their own alarm calls (Trefry and Hik 2009). Trefry and Hik (2009) suggest that this is because yellow-bellied marmots share some, but not all predators of the collared pika. In contrast, Diana and Campbell's monkeys respond equally to their own, as well as each other's alarm calls. They consider the others alarm call as effective as their own, and is likely because they share predators (Zuberbühler 2000a). Regardless of its development or extent of use, eavesdropping clearly holds a fitness advantage for the eavesdropper, and has become an integral part of many species' continued survival.

#### 1.4 Landscapes of Fear

Predators affect prey in both direct and indirect ways (Brown 1999; Creel and Christianson 2007). Directly, predators capture, kill and consume prey (Brown 1988; Brown 1999; Creel and Christianson 2007). Indirectly, predators scare prey with the possibility of being attacked (i.e. perceived predation risk) (Creel and Christianson 2007). This fear has been a dominant force in prey species' life histories, and has been known to drive habitat use (Preisser *et al.* 2005; Laundré *et al.* 2010) and evolutionary

change (Schultz and Noe 2002; Creel and Christianson 2007; Cresswell 2008). Effects on prey species can be varied and extensive. Thus, often perceived predation risk effects are underestimated, or simplified (Preisser *et al.* 2005). Additionally, designing experiments to measure the full range of effects of perceived predation risk can be difficult (Creel and Christianson 2007). However, it is vital to understand the effect of this risk, as this is often quite substantial (Schultz and Noe 2002; Preisser *et al.* 2005; Creel and Christianson 2007).

Ultimately, prey animals aim to avoid predation, and not just escape it when it arises (Lima and Dill 1990). As a result, through their anti-predator behaviour, prey species reveal patterns of perceived predation risk in two or three dimensions (Laundré *et al.* 2001; Laundré *et al.* 2010, Makin *et al.* 2012). These patterns can be termed as ‘landscapes of fear’ (Laundré *et al.* 2001).

Measuring a landscape of fear is one method to evaluate perceived predation risk effectively. A landscape of fear is simply a concept used to quantify how prey animals perceive the environment spatially with regards to predation risk (Laundré *et al.* 2001). Within this landscape, areas perceived to be safe will be used more extensively (e.g. foraging, sleeping) than those perceived to be unsafe (Laundré *et al.* 2001; Laundré *et al.* 2010). A landscape of fear can vary temporally (Brown and Kotler 2004; Fischhoff *et al.* 2007), spatially (Laundré *et al.* 2001) and according to the information available to the prey species (Lind *et al.* 2005).

Changes in predation risk can be found in time scales ranging from days to months. For example, plains zebra (*Equus burchelli*) alter their foraging behaviour daily to avoid lion (*Panthera leo*) predation (Fischhoff *et al.* 2007). During the day, they forage in woodlands and in the evening, they move to open grasslands where they can more easily see approaching predators. These daily movements decrease their risk of capture by lions (Fischhoff *et al.* 2007). Allenby’s gerbil (*Gerbillus allenbyi*) and the greater Egyptian gerbil (*Gerbillus pyramidum*) shifted their foraging effort monthly following the moon cycle (Kotler *et al.* 1991). Increased illumination from moonlight (such as during full and new moons) caused both gerbil species to forage less due to an increased predation risk from increased illumination (Kotler *et al.* 1991).

In addition to temporal changes, predation risk can alter the way prey animals utilize both coarse and fine spatial scales (Tolon *et al.* 2009). Coarse-scale movements involve shifting home ranges in response to perceived predation risk, while fine-scale responses are reflected in localized landscape shifts within the current home range (Tolon *et al.* 2009). For example, Willems and Hill (2009) found that on a coarse-scale vervet monkeys shifted their range use to avoid predation from leopards and chacma baboons (*Papio ursinus*). While on a fine-scale Makin *et al.* (2012) found that vervet monkeys altered their vertical space use and foraged more intensely in trees than in open exposed grassland areas, in an attempt to avoid areas where local risks from predators was higher.

The information available to prey species can also influence how they utilize space. For example, domestic goats (*Capra hircus*) perceived a higher predation risk when caracal (*Caracal caracal*) dung and urine was present among their foraging patches (Shrader *et al.* 2008). The presence of this olfactory information ultimately influenced how the goats used their landscape. Alarm calls can also influence perceived predation risk, which in turn influences the landscape of fear (Lind *et al.* 2005). For example, great tits (*Parus major*) decreased their activity levels and became more wary due to a increased perceived predation risk caused by mobbing from conspecifics (Lind *et al.* 2005). When perceived predation risk is increased, this may influence the landscape use.

Temporal and spatial shifts, as well as information available are not mutually exclusive. Tolon *et al.* (2009) provide an example of wild boars (*Sus scrofa*) shifting their landscapes on both temporal and spatial scales. Humans hunt wild boars seasonally. This provides an increased risk in the hunting season (September – January annually) (Tolon *et al.* 2009). Tolon *et al.* (2009) found that on a coarse scale those wild boar with home ranges that incorporated protected reserves (safe from human hunting) only used the protected area section of their range during hunting season. Those individuals whose home ranges did not incorporate protected reserves had to rely on fine-scale landscape shifts to reduce predation risk (Tolon *et al.* 2009). These individuals used forested patches, which were perceived as safer, during the daytime (when hunting commenced) and open grassland areas at night (when hunting ceased).

Additionally, information available to the wild boars influenced their response to the hunting season (Tolon *et al.* 2009). Those wild boars without contact to the protected reserve were naïve to its benefits. According to Tolon *et al.* (2009) the boar were physically able to use these areas, as they were within their daily movement range. However, their lack of knowledge regarding the protected areas (i.e. they had never been there) limited their use. In this manner, the information available to individuals influenced how they used their landscape in time and space.

Laundré *et al.* (2010) examined predator efficiency throughout the literature, and found on average hunting success for a range of predators was between 8-26%. Thus, when attacks fail, prey species are able to learn about predators and unsafe areas across the landscape (Laundré *et al.* 2010). As a result, prey species adjust their behaviour and thus landscape use in response to specific predator threats (Brown and Kotler 2004). An example of this is the Elk population (*Cervus canadensis*) in Yellowstone National Park, which after the reintroduction of gray wolves (*Canis lupus*) used safer forested patches significantly more than riskier open meadows (Hernández and Laundré 2005).

Landscapes of fear can be measured in a number of ways, including vigilance- and foraging-based methods (Laundré *et al.* 2010). The foraging-based method has become increasingly popular in the last two decades. This method rests on the concept that animals feed more intensely where they feel safe (Brown 1988; Lima and Dill 1990). Thus, depletable food patches are a means to measure a prey animal's landscape of fear in a quantifiable manner (Brown and Kotler 2004). Prey animals need to balance hunger and safety (Brown and Kotler 2004), and thus ensure that they meet their nutritional needs (Lima and Dill 1990; Brown and Kotler 2004). They can therefore change when and how they forage (Lima and Dill 1990). Similarly, Sykes' monkeys (*Cercopithecus albogularis*) forage more intensely in the early morning and late afternoon, and avoid midday, as this is when eagles primarily hunt utilising strong thermals and increased visibility (Emerson *et al.* 2011).

The amount of information available to prey animals influences their landscape of fear (Lind *et al.* 2005). In circumstances when there is no evidence of predator presence (e.g. visual or olfactory cues), prey species still maintain a minimum degree of anti-predator behaviour. This minimum level can be defined as a 'baseline' landscape of

fear. If, however, there is evidence of predators, they may become more cautious (Shrader *et al.* 2008). Therefore, prey animals constantly need to update their risk profile and alter their behaviour in response to this (Bell *et al.* 2009). Predator cues come in many forms including visual, olfactory and auditory signals, and prey species need to be aware of these at all times (Bell *et al.* 2009). Alarm calling or eavesdropping on alarm calls is one reliable method of obtaining information on predator presence. In this study, I investigated how vervet monkeys' landscape of fear changed when they heard various bird alarm calls.

### 1.5 Vervet Monkeys

Vervet monkeys are the most common African primate, and are found in a variety of habitats, including savannah, woodland, forest, semi-desert and urban environments (Cheney and Seyfarth 1990). They live in troops of between 5 – 40 individuals; comprising of all age and sex classes and often encompass many related females (Struthsaker 1967b; Struthsaker 1967c). They actively defend territories (Struthsaker 1967b), which range from 11 – 100 ha (Cheney and Seyfarth 1981; Lee and Hauser 1998).

Several main predators are responsible for the majority of mortality in vervet monkeys (Cheney and Seyfarth 1981). Terrestrial predators include leopards, caracal, serval (*Leptailurus serval*) and other opportunistic ground-dwelling carnivores (Seyfarth *et al.* 1980a; Seyfarth *et al.* 1980b). Their aerial predators are martial (*Polemaetus bellicosus*) and crowned eagles (*Stephanoaetus coronatus*) (Seyfarth *et al.* 1980b; Cheney and Seyfarth 1981; Willems and Hill 2009). Snakes are a threat to vervets as they can inflict poisonous and often fatal bites, but only the African Rock python (*Python sebae*) actively preys on vervets (Willems and Hill 2009). Finally, several species of sympatric baboons (Genus: *Papio*) have also been known to prey on vervets (Cheney and Seyfarth 1990; Willems and Hill 2009). This multitude of predators provides a significant predation risk to the vervets, which they can mitigate by adjusting space use across the landscape (Makin *et al.* 2012).

As stated previously, vervet monkeys have had their baseline landscape of fear mapped on both a coarse (Willems and Hill 2009) and fine (Makin *et al.* 2012) scale with regards to different predators. Willems and Hill (2009) mapped a vervet troop's range use in relation to local predators. They found that the troop spent less time in areas they perceived to have a high predation risk from baboons and leopard. In contrast, local eagle and snake densities did not have an effect on the vervets range use. Willems and Hill (2009) suggested this was due to eagles' flight allowing them to access all areas, therefore on a coarse scale vervets cannot spatially reduce an eagle threat, regardless of home range use (Willems and Hill 2009). Snakes on the other hand, provide a danger to be considered, yet do not actively hunt vervets (with the exception of the African rock python), therefore they did not influence the vervets enough to shift range use (Willems and Hill 2009).

On a small scale, the situation is somewhat different. Makin *et al.* (2012) determined the baseline landscape of fear of vervet monkeys on a fine scale using a patch foraging method. It is beneficial for vervets to maintain this baseline, because they can never fully be free from the risks of predation. For instance, they cannot escape to a burrow or den like sciurid and murid rodents or birds, as suggested by many predation risk models (Brown and Kotler 2004). The vervets' daily range use therefore reflects how they perceive their environment with regards to a constant predatory threat. Makin *et al.* (2012) determined how the vervets' landscape use changed between the trees and open grassland.

Vervets can extend their landscape of fear into both vertical and horizontal planes, as they spend equal amounts of time foraging within trees and along the ground (Cheney and Seyfarth 1990). For this reason, Makin *et al.* (2012) mapped the vervets landscape of fear along the transitional zone between woodland (vertical plane) and grassland (horizontal plane). They found that vervets reduce predation risk by primarily shifting vertically within trees. Across this three-dimensional landscape, vervets used the tops of the trees significantly less than the inner sections under the canopy (Makin *et al.* 2012). Makin *et al.* (2012) hypothesised that the top of the tree is more vulnerable to aerial attack due to increased domains of danger (Hamilton 1971), and is therefore avoided. In contrast, the safest zone in the tree was under the canopy, but up off the

ground, as it likely provides protection from both terrestrial and aerial predators (Makin *et al.* 2012). The grassland further away from the tree was used less than the grassland close to the base of the tree. This is because escape into the trees became harder the further from the trees the vervets ventured (similar to retreating to a burrow for safety) (Makin *et al.* 2012).

### 1.6 Vervet Alarm Calls, Landscapes of Fear, and Eavesdropping

The many predators of vervet monkeys have various hunting strategies (Zuberbühler *et al.* 1999a). Eagles swoop down from the sky and take exposed vervets (Cheney and Seyfarth 1990). They are also able to take vervets from within the trees, as they are skilled and agile fliers (Cheney and Seyfarth 1990; Schultz and Noe 2002). Eagles are central place foragers, so eagle encounters may be greater depending on the proximity to eagle nests (Schultz and Noe 2002). Leopards, and other terrestrial carnivores, are ambush predators, and pounce from the ground (Cheney and Seyfarth 1990). Baboons attack primarily from within the trees and pythons generally from the ground (Cheney and Seyfarth 1990; Isbell 1994)

Due to such varied hunting strategies, vervet monkeys have developed acoustically distinct referential alarm calls for each predator class (Struthsaker 1967a; Seyfarth *et al.* 1980a). Three different alarm calls denote terrestrial predators, aerial predators, and snakes (Seyfarth *et al.* 1980a). Occasionally vervets alarm call for baboons, yet these are less distinct, quiet, and the vervets response is very subtle, as they try to avoid giving away their location (Cheney and Seyfarth 1990). The main three alarm calls are acoustically distinct (Seyfarth *et al.* 1980b), and easily recognisable to human ears, which allow playback experiments to work successfully on vervets (Cheney and Seyfarth 1980b; Seyfarth and Cheney 1990). Additionally, vervet monkey alarm calls are honest signals as they do not alarm unless they have visual confirmation of a predator (Cheney and Seyfarth 1985b; Cheney and Seyfarth 1988). Occasionally mistakes are made, yet these are predominantly from infants or juveniles who are still learning the appropriate calls (Seyfarth *et al.* 1980b; Cheney and Seyfarth 1988).

Seyfarth *et al.* (1980a) found that vervets respond to these different calls with specific behaviours. For example, when the aerial alarm call is heard vervets run into the bushes to avoid eagle detection and attack. In contrast, when the terrestrial alarm call is made, vervets run up into the trees to avoid an ambush from a ground-dwelling predator (Seyfarth *et al.* 1980a). Finally, if a snake alarm call is made the vervets actively look to the ground and scan their surroundings, yet do not adjust their location within the landscape (Cheney and Seyfarth 1980b). The responses to aerial and terrestrial predators are distinctive and locomotive, therefore both easily recorded and influential on foraging efficiency, making them ideal subjects for experimental manipulation of the vervets' landscape of fear.

In addition to responding to their own alarm calls, vervets have been found to eavesdrop on the alarm calls of the superb starling (*Spreo superbus*) in Amboseli National Park, Kenya (Cheney and Seyfarth 1985a). Similar to vervets, superb starlings have specific aerial and terrestrial alarm calls (Cheney and Seyfarth 1985a). Cheney and Seyfarth (1985a) found that vervets recognise these specific alarm calls, and react as if that type of predator was in the area. Cheney and Seyfarth (1985a) observed that when the vervets heard the superb starling's aerial alarm, they looked to the sky, and when the terrestrial alarm was heard, they ran into the trees. This is an example of how vervets respond to functionally referential calls of another species, but what other, less specific signals elicit responses from these clever primates?

Cheney and Seyfarth (1985a) ran a series of experiments to determine what information vervet monkeys acquired regarding indirect cues from predators. They found that the only positive responses from the vervets (that is, the vervets recognising an increased predation risk) were during vocal communications from other species. In addition to reacting to superb starlings' calls, Cheney and Seyfarth (1985a) found some indications (yet not a significant difference) that alarm calls by the black winged stilt (*Himantopus himantopus*) increased vervet vigilance.

In contrast to auditory signals, vervets did not respond to indirect visual predator cues (e.g. spoor). Vervets did not show any recognition of fresh or artificial python tracks, which were an indication of a nearby python (Cheney and Seyfarth 1985a). Nor did they realise that a fresh carcass in a nearby tree indicated the local presence of a



leopard (Cheney and Seyfarth 1985a). Ultimately, vervet monkeys seem better able to process auditory signals compared to visual ones (Cheney and Seyfarth 1985a; Seyfarth and Cheney 2003). This different ability to process these cues provides some insight into the evolution of primate intelligence. Ultimately, for primates, intelligence evolved to solve social problems (Seyfarth and Cheney 2003). Among social communication types, auditory communication became dominant, due to its advantages of being able to communicate over distance and without visual contact (Seyfarth and Cheney 2003; Fichtel and Manser 2010). Vervet monkeys have over 37 distinct vocalizations which are commonly used in social situations (Struthsaker 1967a; Struthsaker 1967c). Therefore it is likely that due to this advanced auditory knowledge, vervet monkeys can readily recognise other species' alarm calls (Cheney and Seyfarth 1985a; Cheney and Seyfarth 2005).

Owren and Rendall (1997) suggest that the vervets learn this recognition in a similar way that rats would in associative conditioning experiments in a laboratory. Specifically, the subject learns the association between a call with an event (e.g. alarm call coupled with the presence of a predator). Over time, the subject then learns to associate just the call with the event, without the actual event occurring (Owren and Rendall 1997). Therefore, it is possible that vervet monkeys have learnt to eavesdrop on a range of species' alarm calls.

### 1.7 Vervets' Perception of Other Species' Alarm Calls

With the exception of the superb starling, it is unknown if vervet monkeys eavesdrop on the calls of other species. With such a wide distribution, vervets are likely exposed to a wide range of other species' alarm calls. Moreover, some of these sympatric prey species (e.g. passerine birds) share similar threats as vervets. Thus, it would provide a fitness advantage to these monkeys to eavesdrop on the alarm calls of these species. However, in contrast to superb starlings, not all species have functionally referential alarm calls. This raises the question of whether vervets are able to associate non-functional referential alarm calls with predation risk. If they can, then the question is do they associate these calls with specific predators, and additionally do they adjust their

behaviour (e.g. landscape use) in relation to that type of predator? To answer these questions, I first determined the vervets' baseline landscape of fear, and how this landscape changed when they heard their own terrestrial and aerial alarm calls. Once I had done this, I explored whether vervet monkeys eavesdropped on the non-referential alarm call of a sympatric bird species, as well as a mixed-flock mobbing call. I then determined how they understood these calls by assessing changes in their small-scale landscape of fear.

With regard to the baseline landscape of fear, I expected the vervets to use their landscape in a similar fashion to that recorded by Makin *et al.* (2012), where they felt safest up in trees just under the canopy. In response to hearing versions of their own terrestrial alarm call, I expected them to shift their foraging to the safest zones up in the tree, and decrease foraging effort on the ground, as recorded by Seyfarth *et al.* (1980a). In contrast, when they heard a vervet aerial predator alarm call, I expected them to perceive the tops of the trees as unsafe and the areas under the canopy and up off the ground as more safe (Seyfarth *et al.* 1980a).

For the sympatric bird species' non-referential alarm call, there were three possibilities. First, if the vervets interpreted the call as denoting an aerial predator, then they should alter their use of the landscape such that it resembles the pattern expressed when the vervets' own aerial predator alarm call was given. Second, if the vervets interpreted the call as a warning of a terrestrial predator I expected that they would follow the terrestrial alarm landscape of fear. The third possibility is that the vervets would not associate the call with a specific predator, and thus move to the safest part of their landscape up in the tree, under the canopy. This would restrict the vervets' use of the landscape to only the ground patches under the canopy.

Finally, with regards to mobbing calls, I suspected that the location of the call would likely be important. As a result, if the call came from the ground, it should simulate the mobbing of a terrestrial predator. Thus, in response, I expected that the vervets would follow their reaction to their own terrestrial predator alarm call. Similarly, if the mobbing call came from up within a tree, it should simulate an aerial predator being mobbed. If the vervets interpret it in this manner, then I would expect the vervets to react as if they had heard their own aerial predator alarm.

## CHAPTER 2: METHODS

### 2.1 Study Site

I conducted this study between April 2012 and March 2013 using three vervet monkey troops at two study sites around Pietermaritzburg, KwaZulu-Natal, South Africa. The first (N=14, group 1, site 1) and second (N=7, group 2, site 2) troops were located at Boulderhill Farm (group 1: 29° 41' 45.75"S, 30° 26' 22.37" E; group 2: 29° 41' 23.37" S, 30° 26' 22.37" E). As vervet monkeys are territorial (Cheney and Seyfarth 1990), the home ranges of troops 1 and 2 did not overlap, and thus the data collected from them were assumed to be independent. The third troop (N=10, group 3, site 3) was located at Bisley Nature Reserve (29° 39' 29.61" S, 30° 23' 57.02" E). The furthest distance between these three troops was 5.7 km. The vegetation type at both study sites comprised sub-arid thorn bushveld (Mucina and Rutherford 2006).

For all three troops, I focused my data collection on the transitional zone between woodlands and open grassland. By including both habitat types, I was able to investigate how vervet monkeys perceive safety vertically in the trees and horizontally along the ground (see Makin *et al.* 2012). Despite being within the same vegetation type, tree species and tree height varied between each site. However, all areas were utilised by vervet monkeys. Site 1 consisted of *Acacia natalitia* trees between 6-8 meters, site 2 comprised *Acacia nilotica* trees between 3-5 m, and site 3 consisted of *Acacia nilotica* trees between 4-6 m.

In contrast to vegetation differences, each site had similar predators. I noted martial and crowned eagles flying above the sites, while landowners in the area have seen caracal, black-backed jackal (*Canis mesomelas*) and domestic dogs (*Canis lupus familiaris*) roaming the area. Thus, at all three sites, vervets were exposed to both terrestrial and aerial predators.

## 2.2 Experimental Design

### 2.2.1 Giving Up Densities

In order to quantify the vervet monkeys' perceived predation risk, I measured giving-up densities (GUDs) from artificial patches. A giving-up density is the amount of food left in a patch once a forager has ceased foraging (Brown 1988). When animals forage, they weigh up the costs and benefits of feeding in a patch. Brown (1988) devised patch foraging rules to explain when an individual should quit feeding within a patch. Ultimately, an animal should continue to feed in a patch provided the harvest rate (H) outweighs the costs of foraging, which includes the cost of predation (P), metabolic cost of foraging (C) and missed opportunity costs (MOC) (Brown 1988). Metabolic costs of foraging incorporate the physiological costs of foraging in a specific area (Brown and Kotler 2004). Missed opportunity costs place a value on alternative fitness enhancing opportunities that the forager may miss while in a specific patch (Brown and Kotler 2004). Ultimately, a forager should choose to leave a patch once the energy gain from a patch (H) is less than or equal to the sum of the associated costs ( $P+C+MOC$ ) (Brown and Kotler 2004).

By keeping the amount of food and effort required to obtain it equal among all patches, the metabolic costs of foraging and missed opportunity costs were equal throughout all patches (Brown and Kotler 2004). Thus, the only varying cost was the perceived predation risk (Brown and Kotler 2004). Therefore, harvest rate (H) was a proxy for predation risk (P), which varied according to the position of the patch. As GUDs can act as an index of H (Schmidt *et al.* 2008), they provide a way to quantify perceived predation risk. A key assumption of using GUDs is that animals forage more intensely where they feel safe compared to where they feel unsafe (Brown 1999). Therefore, a lower GUD (i.e. greater feeding effort) indicates perceived safety, while higher GUDs (i.e. lower feeding effort) indicate areas that are perceived to be unsafe.

### 2.2.2 Experimental Set Up

I used artificial patches similar to that of Makin *et al.* (2012). Each patch was made up of a 5 l white plastic bucket (diameter: 200 mm; height: 170 mm) with a tight sealing lid. I cut a 60 mm circular hole in the centre of the lid, which allowed the monkeys to insert their hands into the buckets and retrieve food. As food, I used ~130 g of unsalted raw shelled peanuts in each patch, as they were easily available and legumes form a natural part of a vervets' diet (Richard 1985). I used 130 g of peanuts as this was enough to attract the monkeys to the patches, but it was not sufficient to permanently alter the vervets' diet (Makin *et al.* 2012). To provide diminishing returns within the patches and thus simulate natural patches, I placed 30 circular wooden discs approximately 10 mm thick and between 65 - 100 mm in diameter into the buckets. As the diameter of these discs was larger than the opening in the lid, the monkeys could not remove them from the buckets. I used 30 discs to ensure that the vervets could not remove all the peanuts and thus I could record GUDs under all experimental conditions.

To establish a baseline of how the vervet monkeys perceived predation risk within and away from a tree into the grassland, I placed eight artificial patches in line transects at each site. Site 1 and 3 consisted of four transects, while site 2 only had three transects. Each transect was separated by 7-10 m. I originally attempted to have an equal number of transects at all sites, however, there was not enough space for four transects at site two.

The placement of seven of the eight artificial patches followed Makin *et al.* (2012, Fig. 1). These included three within the tree, comprising: one at the top of the tree canopy exposed to the sky (patch 2), another just below the canopy (patch 3), and a third halfway down the trunk of the tree (patch 4), approximately 1 m off the ground, where the first branch emanated from the tree (Fig 1). In addition to these three patches, I added a fourth patch on the edge of the tree canopy (patch 1), on the side towards the open grassland (Fig. 1). This patch provided further insight into the vervets' perceived predation risk within the tree. Makin *et al.* (2012) found that the top of the tree canopy was perceived to be the most dangerous area within the tree. This is likely due to an

increased domain of danger (Hamilton 1971). The edge of the tree canopy has a reduced domain of danger, as the vervets are only exposed on the one side, while their other side is protected by the canopy. Therefore, I expected the patch on the edge of the tree canopy to be perceived by the vervets as the second most dangerous area within the tree, following the top of the tree. As with Makin *et al.* (2012), I also placed four patches along the ground. The first was at the base of the tree (patch 5), while the remaining three were 5, 15, and 30 m away from the tree into the grassland (patches 6-8 respectively; Fig. 1).

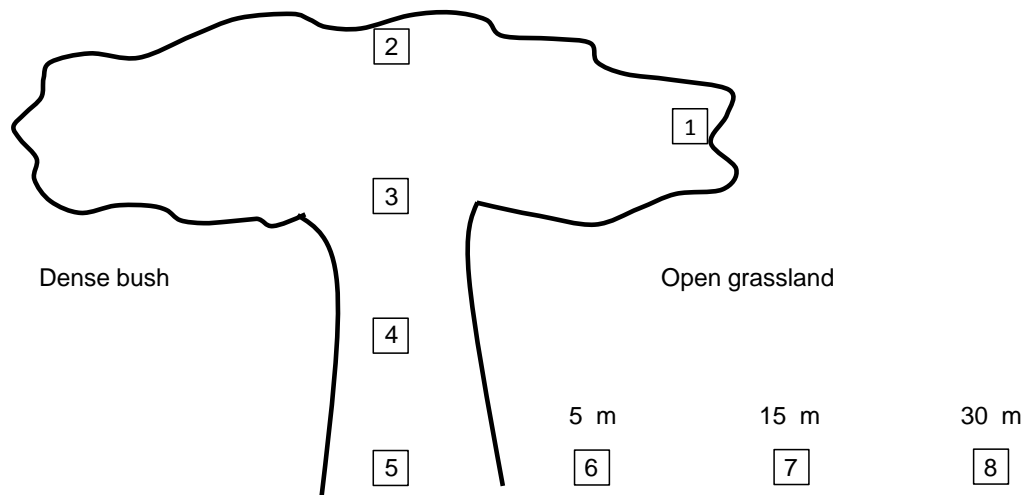


Figure 1: Placement of artificial patches within and away from the trees within each transect. Numbers (1-8) indicate patches.

To ensure that the monkeys did not remove these patches, I attached each patch to branches of the tree using wire. I did this by puncturing four holes in the side of each bucket, and passing wire through the holes. For those along the ground, I attached the patches to 60 cm long metal stakes hammered half way into the ground. Using this set up, I was able to determine how the vervets' perception of fear varied in both vertical and horizontal space. Vervets visited the patches on a daily basis, foraging for between 1-2 hours before moving on. To determine the daily feeding effort, I emptied and refilled the patches each morning between 07h00-08h00, and weighed the remaining

food (i.e. the GUD) in a lab. I excluded days in which the vervets did not forage within the transects.

Prior to data collection, I first habituated the vervets to the experimental set up. Habituation varied between 2-4 months, depending on the troop. Habituation for the first troop commenced in April 2012, and by November 2012, I had habituated all troops to the patches. I waited until all three troops were habituated before I started data collection. Thus, data collection started at all three sites simultaneously in November 2012, and lasted until March 2013. This avoided potential seasonal effects, which may have included deciduous trees losing their leaves resulting in reduced canopy cover. Additionally, this avoided seasonal variation in natural food supply.

The habituation process started with 3 buckets being set out per transect at each proposed site, to determine if the monkeys actually visited these sites. The buckets were attached in the trees at positions 3, 4 and 5 (Fig. 1), which are perceived as the safest zones of the tree (Makin *et al.* 2012), therefore they were the ones most likely to be visited by the monkeys. Initially I put out the buckets without lids or wooded discs. Within these patches, I placed 200-250 g of peanuts to attract the vervets. I checked the patches daily, and refilled when the vervets had eaten the peanuts. Once the vervets were visiting the patches regularly (i.e. at least once every two days), I set up all eight patches in each transect. As before, these patches consisted of just the bucket, without a lid or matrix, and I put 200 – 250 g peanuts in each patch. I left the patches like this for up to a month allowing the vervets' time to investigate and feed regularly from them. For the entire habituation process, I checked the patches daily and refilled when necessary. Once the vervets were habituated to the open patches, I attached the lids to the patches and allowed the vervets to habituate to these closed patches for two weeks. I then added 5 wooden discs to each bucket and allowed the vervets to feed from these partially filled patches for an additional two weeks. I continued this process for six more weeks increasing the number of discs to 10, 20 and finally 30 wooden discs every two weeks. I considered the vervets habituated when they foraged from the patches at least once every two days.

### 2.2.3 Playback Experiments

To quantify how the vervets' space use varied in reaction to increased perceived predation risk, I conducted playback experiments of various alarm calls to manipulate perceived predation risk and recorded GUDs from the artificial patches. Similar to Makin *et al.* (2012), I first determined the vervets' baseline landscape of fear within and away from the tree. For each troop, I collected baseline data for nine days. Ultimately, this provided insight into how the vervet monkeys perceived their environment on a day-to-day basis. Once I had obtained the baseline, I was able to compare the results from the alarm call playback experiments to this baseline landscape of fear to establish how the vervets responded to changes in perceived predation risk.

I was confident in my use of playback experiments as vervet monkeys have been known to respond to playbacks of their own alarm calls, regardless of if a threat is present or not (Cheney and Seyfarth 1990). Moreover, they do not habituate easily to an alarm call, which would result in ignoring it, even if it were repeatedly false (Cheney and Seyfarth 1988). They live in such variable and dangerous habitats that the cost of ignoring a call, even if it is unreliable, is too high (Cheney and Seyfarth 1988). Therefore, playback experiments with vervet monkeys are often very successful (Cheney and Seyfarth 1990).

I played the different alarm calls through two 10 W Boashan horn speakers (Model: SK-610) attached to the trees between transects 1-2 and 3-4, to ensure the vervets heard the call from all transects evenly. I played the calls at amplitudes I deemed to be the natural volume of the call and this was kept constant throughout the treatments. The height within the tree at which I attached the speakers was dependent on the call being played (see below: 2.2.3.2). I played all calls from a 5-core Sound of India amplifier (Model number: 5CA-4040) powered by a 12 V car battery (Leisure Pak, model: FNL 464).

I positioned the amplifier approximately 100 m away from the transects within a bush-hide where I was seated. I played alarm calls when the vervets had moved into the area and had started feeding. I played a call every 10 minutes while the vervets fed creating a heightened risk of predation during the entire feeding bout. Feeding bouts



lasted between 1-2 hours. I used 10-minute intervals between calls as Hauser (1988), in a similar study, observed that vervets stopped responding to superb starling alarm calls a few minutes after they had heard them. Additionally Seyfarth *et al.* (1980b) ceased recording vervet monkey alarm calls after 15 minutes of them first sounding them, as by this time the vervets had resumed normal behaviour. The 10-minute intervals between calls would allow the vervets' time to relax and continue foraging, while still keeping them alert and vigilant for a potential predator throughout their feeding bout.

To prevent the transects being perceived as a constantly dangerous area and thus chasing away the vervets, the playbacks were not conducted on consecutive days. I was only able to conduct one playback experiment per day at a single site. Therefore, while one site was being subjected to a playback experiment the other two sites were experiencing "rest" days, in which I applied no treatment. Therefore, each site had a minimum of two days rest between playbacks. On some occasions, sites had a longer rest, as playback experiments were not conducted on rainy days to avoid potential weather influence. On rest days, I refilled the patches as usual to ensure the vervets remained habituated to the set up, but I did not weigh the remaining peanuts (i.e. collect GUDs) as part of the experiment. Each playback treatment had three replicates on three separate days. I did not play the different calls in a specific order at the three sites, but rather played them in a random order to ensure a single treatment was not conducted on consecutive days. By limiting the number of days the individual playbacks were used, we attempted to minimise any pseudoreplication of the data (Kroodsmas *et al.* 2001).

#### 2.2.3.1 Vervet Monkey Alarms

The first set of playbacks I conducted was of the vervets' own terrestrial and aerial alarm calls. This simulated a troop member identifying a threat and notifying the other troop members. Ultimately, this provided quantifiable measures of the patterns reported by Seyfarth *et al.* (1980a).

Cheney and Seyfarth (1980b) found that vervet monkeys can recognise vocalizations given from individuals within their own troop. For this reason, I originally

wanted to record a terrestrial and aerial predator alarm call from one of the troop members in each troop, and use this for the playback experiments. However, due to logistical and time constraints of the project I was unable to acquire the different calls from each troop. I therefore used the vervet terrestrial and aerial alarm calls recorded by D. Cheney and R. Seyfarth, which I obtained off the internet: <http://pin.primate.wisc.edu> (see Cheney and Seyfarth 1980a). These calls were a single distinct alarm call lasting two seconds which I played once every ten minutes.

Initially, I was concerned that by doing this the vervets may have reacted more to the fact that the calls were from unknown individuals (and thus potentially a rival group invading their territory) rather than to the alarm calls themselves. Cheney (1981) found that when vervets come across a rival group, they first vocalize (acoustically distinct from any predator alarms) to warn their troop and the new troop that they have been seen. They then observe this intruder troop, by increasing vigilance. If a direct encounter arises adults threaten, chase and fight the intruding individuals (Cheney 1981). Therefore, if the vervets interpreted the foreign alarm call as a territory invasion, I would have expected to observe the vervets foraging less and increasing alertness. To test this, I played a trial run of the foreigner's terrestrial and aerial alarm call for each troop, and observed their reaction. I observed that the vervets did not react as if their territory was being invaded, rather they reacted as I expected, following the predator response patterns described by Seyfarth *et al.* (1980a) (See results: 3.2.2.1).

It is possible that the vervets recognised that the alarm call was not from a known individual, yet this did not influence their reaction to the alarm. If this was the case, then the fact that they reacted to the alarm call suggests that the cost of ignoring an alarm was greater than the potential threat of a territory invasion. Ultimately, in such a variable and unpredictable world vervets cannot afford to ignore an alarm call, regardless of its origin.

Similar instances of not being able to ignore an alarm have also been found in other species. For example, male barn swallows (*Hirundo ristica*) gave false alarm calls when their paternity was at stake (Møller 1990). During egg laying, male barn swallows gave dishonest alarms (i.e. no predator present) to disrupt extrapair copulation attempts towards their mates when they had left the nest without them (Møller 1990). This

system worked because the swallows attempting to copulate could not afford to ignore an alarm call, even if it was occasionally dishonest (Møller 1990).

In a similar manner, the vervet monkeys cannot afford to ignore a call signalling the presence of a potential predator. Furthermore, vervets only alarm when they have visual confirmation of a predator (Cheney and Seyfarth 1985b). Unlike the male barn swallows, the vervets have no reason to suspect dishonest signalling. Diana and Campbell monkeys give alarm calls when they hear their own or each other's alarms through playback experiments (Zuberbühler 2001). Therefore, it is possible to elicit an individual alarm calling without the presence of a predator. However, vervets do not alarm call in response to hearing playbacks of their own alarm sounds (Zuberbühler 2001). Rather, they wait until they have visual confirmation of a predator before alarm calling (Zuberbühler 2001). Therefore, when the vervets hear alarms, even ones from unknown conspecifics, they interpret this as an honest signal, indicating a predator has been seen. For this reason vervet monkeys readily respond to playback experiments (Seyfarth *et al.* 1980b; Cheney and Seyfarth 1990), even those of foreign conspecifics, as they have done in this study. With the above points in mind, I am confident that the playbacks that I used have resulted in the behavioural patterns that reflect the vervets' reactions to increased perceived predation risk, and not territorial responses to the calls of unknown individuals.

#### 2.2.3.2 Eavesdropping Playbacks

To determine whether vervet monkeys eavesdropped on bird alarm calls, I used two separate calls. The first call I used was of the local passerine red-backed shrike (*Lanius collurio*). I used the red-backed shrike because it is similar to vervets in that it is preyed upon by both aerial raptors and several terrestrial predators (Newton 1991). Moreover, red-backed shrikes are widely distributed migratory species, found throughout southern Africa in the summer months (Sinclair 1984). Thus, they were prevalent in the study area during my research period between November 2012 and March 2013. The red-backed shrike's alarm call is a distinct "chak-chak" sound, which is called when a potential threat is identified (Sinclair 1984). However, it is not predator-specific

(Sinclair 1984). I obtained the recording of the alarm call from Mr. Doug Newman, a local bird expert and author of the bird call book, “500 common bird calls in southern Africa” (Newman 2013).

Following Schmidt *et al.* (2008), I used a mixed-species flock bird mobbing call to indicate predator presence. Mixed-species mobbing calls consist of a collaboration of birds sounding acoustically similar calls at a potential predator (Johnson *et al.* 2003) and are intended for both conspecifics and heterospecifics (Randler and Förschler 2011). The call is standard for all types of threats, terrestrial or aerial (Johnson *et al.* 2003). Due to the general nature of mobbing calls, I did not limit my search to the mobbing call of local species, as heterospecifics do not recognise specific species during mobbing bouts (Johnson *et al.* 2003). Thus, I used a readily available mixed-species flock mobbing call directed at an eastern screech owl (*Megascops asio*) which I obtained off the internet: <http://pjdeye.blogspot.com> (see Driver 2010). Both the mobbing call and the red-backed shrike call were played for a duration of 30 seconds every ten minutes.

I did not use calls of specific vervet predators, such as the call of a crowned eagle, because in a similar study, Schmidt *et al.* (2008) found that eastern chipmunks did not respond to calls of their direct predator, the broad-winged hawk (*Buteo platypterus*). Schmidt *et al.* (2008) reasoned that this was because predator calls give away location, identity and state of the predator, therefore enough information had been obtained by the eastern chipmunks for them to not deem the caller a threat. Furthermore, hunting animals do not give away their intentions by signalling, therefore predators that are indeed calling are not seen as an immediate threat, and thus their calls are not responded to (Schmidt *et al.* 2008). I reasoned that the same situation would occur with the vervet monkeys. If they heard a direct predator call, they would not respond to the call, so I did not use specific predator calls as a treatment.

Finally, to test whether the speakers were influencing the behavioural responses of the vervets, I played a red-eyed dove contact call as a control. This is an obvious, regularly heard, local call, which should not elicit a fear response from the vervets. As with the red-backed shrike, I obtained this call from Mr. Doug Newman.

I played the vervets' terrestrial and aerial calls, the red-backed shrike alarm call, as well as the red-eyed dove contact call from mid-tree height, approximately 2-3 m off the ground depending on tree height. To simulate the presence of aerial and terrestrial predators, I played the mobbing call from two different locations by shifting the location of the speakers. To simulate a terrestrial predator being mobbed, I played the mobbing call from the ground. In contrast, to simulate an aerial predator being mobbed I played the same mobbing call from the top of the tree. For all treatments the speakers were attached to the trees between transects 1-2 and 3-4.

### 2.3 Animal Ethics

This study followed the University of KwaZulu-Natal animal ethics protocol. The Animal Research Ethics Committee granted approval for the study in 2012 and 2013, and awarded the reference numbers 055/12/Animal and 018/13/Animal respectively.

### 2.4 Statistical Analyses

The transects within each site were not independent replicates, therefore a mean GUD for each position (i.e. patches 1-8) was determined per day (N= 9 days for the baseline; N=3 days for vocalization treatments). Sample size was 648 mean GUD patches. The foraging of the same troops (troop 1, 2 and 3) were measured each day. Therefore, the experience of a previous day could influence how the vervets foraged the following day. To account for this in the analysis, I considered troop as a repeated measure. The GUD data followed a gamma distribution, and lacked homogeneity of variance. Therefore, to account for these parameters and the repeated measures, I used Generalized Estimating Equations to investigate how GUDs varied in response to the different alarm calls. Factors in the model included Position (1-8) and vocalization (1. baseline, 2. aerial, 3. terrestrial, 4. red-backed shrike, 5. dove, 6. mobbing up and 7. mobbing down). I included the interaction of these to determine how positions differed according to the various vocalization treatments. As I was not interested in between troop differences, I accounted for the inherent effect of different troops by adding troop as a covariate. I

used a Sequential Sidak multiple comparisons test to generate marginal means. I carried out all analyses using IBM SPSS Statistics 21.

## CHAPTER 3: RESULTS

### 3.1 Overall Pattern

Across all variables, perceived predation risk significantly affected foraging effort (mean GUDs) of the vervet monkeys within the 3-dimensional landscape. There were significant differences in foraging effort between troops ( $\chi^2_{1,648} = 45.7$ ;  $p < 0.0001$ ), patch ( $\chi^2_{7,648} = 19.9$ ;  $p = 0.006$ ), vocalization ( $\chi^2_{6,648} = 14.5$ ;  $p = 0.025$ ), and the interactions of patch and vocalisation ( $\chi^2_{55,648} = 67.1$ ;  $p = 0.008$ ).

#### 3.1.1 Baseline

Not surprisingly, the vervet monkey's baseline landscape of fear was similar to Makin *et al.* (2012) (Fig. 2). Overall, the vervets preferred the patches within the trees (mean GUD  $\pm$  SE:  $65 \pm 4$  g) compared to patches in the grasslands (mean GUD  $\pm$  SE =  $105 \pm 7$  g, Fig. 2). They foraged most intensively (i.e. achieved the lowest GUDs: mean  $\pm$  SE  $56 \pm 5$  g) just under the canopy at the main fork of the tree. As with Makin *et al.* (2012), this represented the safest zone within the landscape (Fig. 2). Surprisingly, the vervets considered the patches at the edge of the canopy (patch 1: mean  $\pm$  SE:  $74 \pm 4$  g) less safe than the patches at the top of the canopy (patch 2: mean  $\pm$  SE:  $63 \pm 5$  g). As expected, foraging effort in the grassland decreased with increasing distance from the trees, with the safest zone at the base of the tree, and least safe 30 m out into the grassland (Fig. 2).

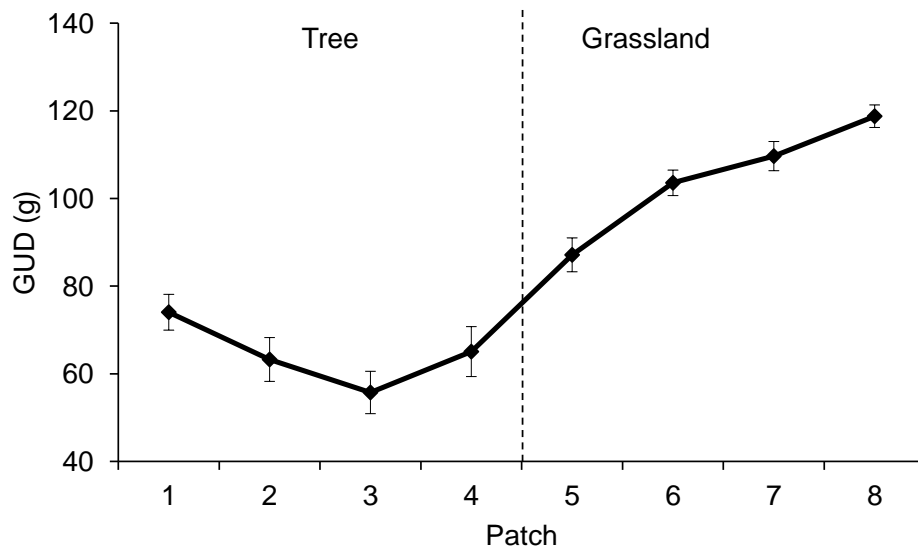


Figure 2. Mean ( $\pm$ SE) giving up densities for the baseline across the 3-dimensional landscape located within the tree and along the ground (i.e. patches 1-8).

### 3.2 Playback Experiments

#### 3.2.1 Control: Dove Call

When I played the dove call, the vervet monkeys' feeding effort across the landscape did not change in relation to the baseline (Patches 1-8  $p = 1.000$ , Fig. 3). This indicates that the monkeys did not react to the speaker setup.



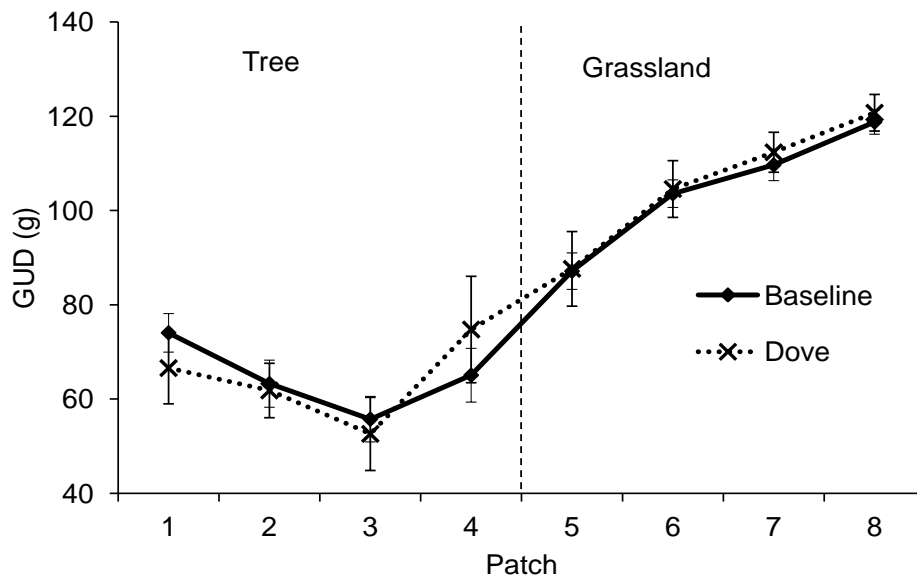


Figure 3. Mean ( $\pm$ SE) giving up densities for the baseline and dove playback treatment across the 3-dimensional landscape located within the tree and along the ground (i.e. patches 1-8).

### 3.2.2 Vervet Monkey Alarm Calls

#### 3.2.2.1 Reactions to Foreign Alarm Calls

When I played the terrestrial alarm call, the vervets' vigilance seemed to increase, directed particularly towards the ground. Those on the ground at the time moved towards the trees. This was an appropriate escape response for the vervets, indicating that they perceived the alarm call as a warning of a predator and not as a territory threat (see section 3.2.2.2). Similarly, when I played the foreign vervet aerial alarm, the vervets seemed to be on high predator alert and look towards the sky (see foraging detail in section 3.2.2.3). This suggests that they focused on the alarm aspect of the call and not the identity of the individual making the call. It is possible that the troops realised that the alarm calls came from an individual not from their troop, yet this did not seem to influence the vervets' reaction to the alarm.

### 3.2.2.2 Terrestrial Predator Alarm Call

The vervets responded to the terrestrial alarm call in a manner similar to that described by Seyfarth *et al.* (1980a). When compared to the baseline, they fed less intensively (i.e. achieved higher GUDs) in areas away from the tree (Fig. 4). Specifically, the mean difference among pairwise comparisons indicated that in patches 5 -7 feeding effort declined significantly (Patch 5  $p = 0.029$ , Patch 6  $p = 0.053$ , Patch 7  $p = 0.005$ ), while in patch 8 feeding effort did not change ( $p = 0.770$ , Fig. 4). In contrast, feeding effort increased in the canopy of the tree (Patch 1  $p < 0.0001$ , Patch 2  $p = 0.007$ ; Fig. 4), indicating that the vervets considered these areas safer than being close to the ground. However, the use of the inner and middle sections of the trees (i.e. patches 3 and 4) which were closer to the ground did not differ from the baseline pattern (Patch 3-4  $p = 1.000$ , Fig. 4).

### 3.2.2.3 Aerial Predator Alarm Call

As with the terrestrial alarm call, I found that in response to vervets' aerial predator alarm call the vervets foraged in a pattern that matched the behavioural responses described by Seyfarth *et al.* (1980a). Moreover, this pattern differed to the baseline pattern. As expected, feeding effort decreased significantly at the top of the canopy (Patch 2  $p < 0.0001$ ), but surprisingly not on the side of the canopy (Patch 1  $p = 0.114$ ; Fig. 4). As in response to the terrestrial predator alarm call, the vervets used the remaining zones within the tree in the same manner as they did in the baseline landscape (Patch 3  $p = 1.000$ , Patch 4  $p = 1.000$ , Fig. 4). Moreover, they also fed significantly less intensively away from the trees than in the baseline landscape (Patch 5  $p = 0.002$ , Patch 6  $p = 0.029$ , Patch 7  $p = 0.002$ ), with the exception of patch 8 ( $p = 0.208$ , Fig. 4).

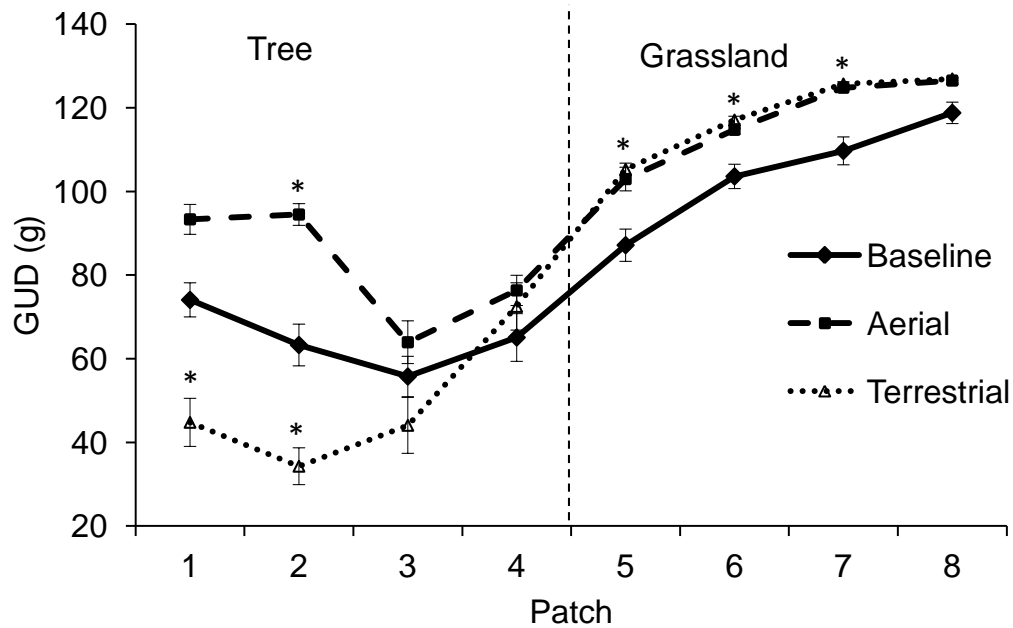


Figure 4. Mean ( $\pm$  SE) giving up densities of baseline, aerial alarm and terrestrial alarm treatments across the 3-dimensional landscape located within the tree and along the ground (i.e. patches 1-8). \* indicates a significant difference to the baseline.

### 3.2.3 Eavesdropping

#### 3.2.3.1 Red-backed Shrike

When testing whether the vervets eavesdropped on the red-backed shrike alarm call, I found that they did not alter their feeding intensity from the baseline (patch 1-2  $p = 1.000$ , patch 3  $p = 0.901$ , patch 4  $p = 1.000$ , patch 5  $p = 0.359$ , patch 6  $p = 1.000$ , patch 7  $p = 0.868$ , patch 8  $p = 0.752$ , Fig. 5).

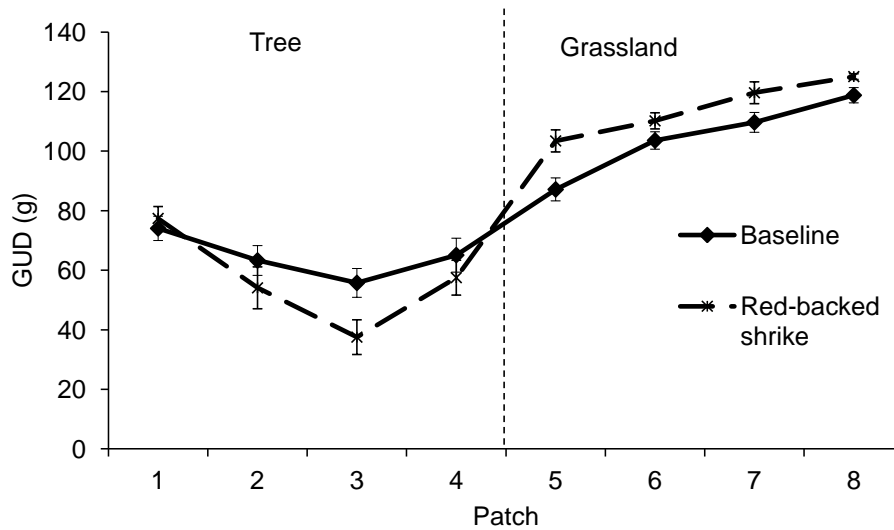


Figure 5. Mean ( $\pm$ SE) giving up densities for the baseline and red-backed shrike treatments across the 3-dimensional landscape located within the tree and along the ground (i.e. patches 1-8).

### 3.2.3.2 Mobbing Up

I compared the mobbing call from up the tree to the aerial alarm to determine if the vervets eavesdropped on this call and associated it with an aerial predator. As predicted, I found no difference between these two calls (Patches 1 and 3-8  $p = 1.000$ ; Patch 2  $p = 0.799$ , Fig. 6).

### 3.2.3.3 Mobbing Down

When simulating a terrestrial predator by playing the mobbing call from the ground, I found that the vervets' feeding pattern was the same as when I played the vervets' terrestrial predator alarm call (Patches 2-8  $p = 1.000$ , Fig. 6). The only difference was at the edge of the canopy where the mean difference showed that feeding effort declined significantly (i.e. higher GUDs) from the baseline ( $p < 0.0001$ ).

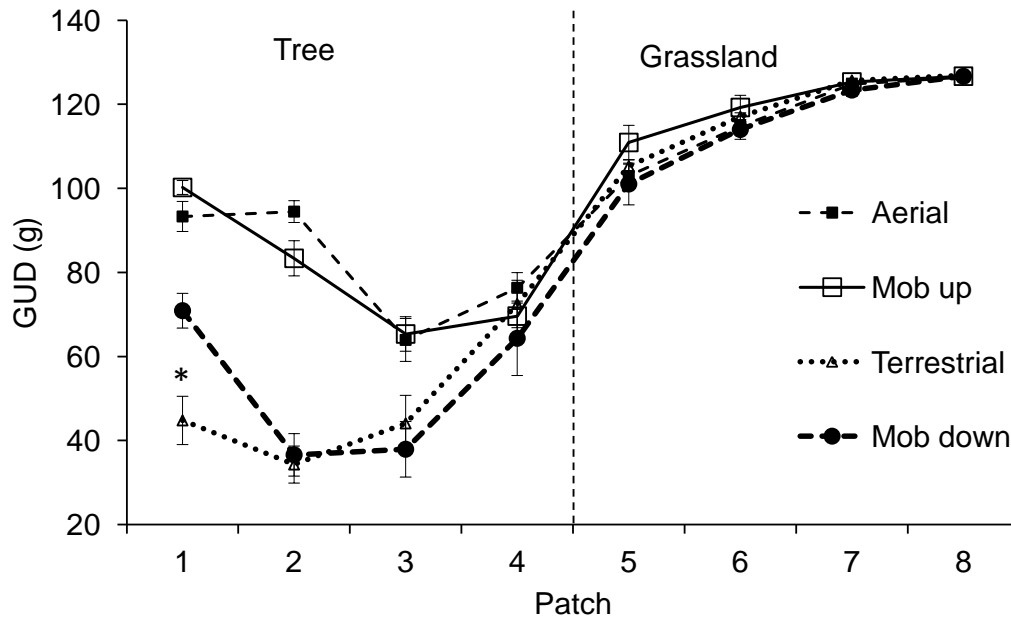


Figure 6. Mean ( $\pm$  SE) giving up densities of eagle and leopard alarm call treatments, and mobbing treatments from up in the tree and down on the ground across patches 1-8. \* indicates a significant difference between the vervets' alarm call (e.g. terrestrial) and the mobbing call (e.g. mobbing call played from the ground).

### 3.2.4 Total Food Eaten

The total amount of food eaten for each treatment (i.e. removing the patch effect) was mostly – but not entirely – similar among different treatments. Specifically, when compared to the baseline (mean  $\pm$  SE:  $85 \pm 2$  g), vervets ate similar amounts of food in response to the dove call (mean  $\pm$  SE:  $85 \pm 3$  g;  $p = 1.000$ ), red-backed shrike (mean  $\pm$  SE:  $86 \pm 5$  g;  $p = 1.000$ ), terrestrial alarm call (mean  $\pm$  SE:  $84 \pm 5$  g;  $p = 1.000$ , Fig. 7), and the mobbing call played from the ground (mean  $\pm$  SE:  $84 \pm 4$  g;  $p = 1.000$ ) (Fig. 7). In contrast, the vervets ate significantly less food across the landscape in response to the aerial predator treatment (mean  $\pm$  SE:  $100 \pm 4$  g;  $p = 0.0001$ ), and the mobbing call played from up in the tree (mean  $\pm$  SE:  $100 \pm 3$  g;  $p = 0.002$ ) (Fig. 7). Furthermore,

overall foraging effort did not differ significantly between the aerial predator call and the mobbing call from up in the tree ( $p = 1.000$ , Fig. 7).

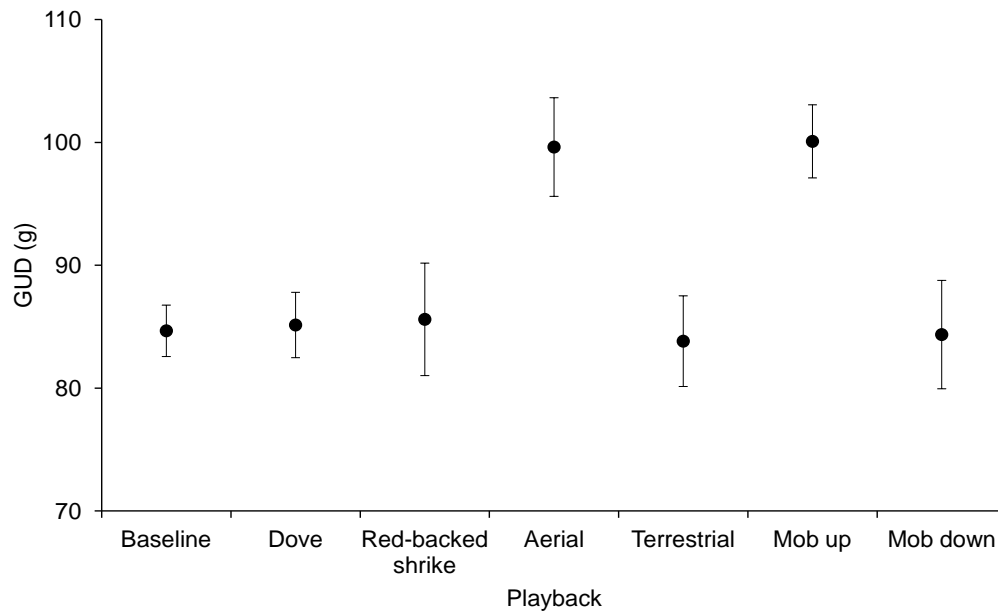


Figure 7. Combined giving up densities (Mean  $\pm$  SE) of all eight artificial patches within the different playback treatments.

## CHAPTER 4: DISCUSSION

Prey animals perceive fear in their environment, and alter their landscape use in an attempt to limit predation risk (Laundré *et al.* 2010). Additionally, external stimuli such as alarm calls can influence prey animals perception of fear (Schmidt *et al.* 2008) and hence their landscape use. I found that vervet monkeys perceived predation risk in their immediate environment and in response shifted their foraging behaviour in relation to that risk. As found by Makin *et al.* (2012), the baseline landscape of fear recorded in my study illustrates that the vervets find trees safer than open grasslands. Additionally, perceived predation risk increased the further away from the trees they ventured. As expected, the vervets altered their landscape of fear when they perceived an immediate threat in their environment, such as in response to conspecific alarm calls. For example, when the vervets heard the terrestrial predator alarm call, they shifted their foraging away from the ground, and concentrated their feeding (i.e. achieved lower GUDs) up within trees. When they heard the aerial predator alarm call the vervets shifted their feeding intensity in an effort to avoid the exposed areas of the tree, as well as the open grassland. In addition to responding to their own species alarm calls, vervet monkeys also responded to heterospecific mobbing calls, but not the alarm call of the red-backed shrike. As predicted, when the vervets heard a mixed-species bird mobbing call from the ground they responded as if a terrestrial predator was nearby. When they heard the same mobbing call from up in the tree, they responded as if an aerial predator, such as an eagle, had been seen. These responses suggest that vervets are able to make links between the location of non-specific alarm calls and the potential specific predator types, and then react accordingly so as to reduce predation risk. They perceived these heterospecific alarm calls as clear warning signs of specific danger, by using the location of the call to grasp information about the potential predatory threat.

### 4. 1 Baseline Landscape of Fear

The vervet's baseline landscape of fear followed Makin *et al.* (2012), who were the first to use GUDs to map the small-scale perceived predation risk of vervet monkeys. The

monkeys foraged in the trees more intensely than the open grassland, and decreased their foraging effort with increasing distance from the tree line. In addition to the original landscape measured by Makin *et al.* (2012), I added a patch on the edge of the tree canopy to provide additional insights into the monkeys horizontal use of the tree canopy. Surprisingly, the vervets used this patch the least amongst the within-tree patches.

Vervet monkeys have to escape from several predators (Cheney and Seyfarth 1990). Their main predators consist of terrestrial predators, such as leopards or caracal, and aerial predators, such as martial or crowned eagles (Seyfarth *et al.* 1980a; Willems and Hill 2009). This threat drives how vervets use their small-scale space on a day-to-day basis. Although predation risk can vary within space and time (Brown 1999; Brown and Kotler 2004), this use of space seems to be fairly consistent, as the overall pattern has changed little in the three-year gap between the work of Makin *et al.* (2012) and this study.

With regard to the baseline, the centre of the tree at the main fork of the canopy was utilised most extensively (i.e. lower GUDs were achieved). This suggests that the vervets considered this area safer. This is likely as this area represents the safest area from both classes of main predators (Makin *et al.* 2012). Terrestrial predators, such as leopards, are ambush hunters which strike from the ground (Cheney and Seyfarth 1990). Therefore, up in the canopy of the tree is safest from this form of attack. Although leopards are skilled tree climbers (Cheney and Seyfarth 1990), the vervets' agility within the trees far out skills a leopard's (Cheney and Seyfarth 1990), so vervets likely consider staying in the trees safer.

In contrast to terrestrial predators, eagles can effectively swoop down and take vervets from either the ground, or from within the trees (Seyfarth *et al.* 1980b; Cheney and Seyfarth 1990). For this reason, no area within the vervets' 3-dimensional landscape is completely safe from eagles. However, the vervets considered some areas safer than others. Vervets consider areas exposed to the sky less safe than those under cover. Eagles can take exposed vervets from the tops or sides of the tree, or from the open grassland (Cheney and Seyfarth 1990), therefore to avoid predation the vervets preferred to stay under the cover of the canopy. Schultz and Noe (2002) found that out



of six monkey species (not including vervets) Diana monkeys are found highest in the tree canopies and suggested that they are at the highest risk from aerial predators because of this position. This suggests that the top of the tree canopy is not a safe area when aerial predators are hunting. Because of this, vervets use the tops of the trees, and the exposed grassland significantly less than the centre of the tree.

The centre of the tree (patch 3), is covered by the canopy, which provides visual protection from eagles, thus the vervets consider this patch safest. This is in contrast to what Emerson *et al.* (2011) found with Sykes' monkeys. In a similar experiment, also using GUDs to map the monkeys landscape of fear, Emerson *et al.* (2011) found that GUDs declined with height in the tree. Therefore, the tops of the trees, unlike in this study, were considered safer by Sykes' monkeys. This is not remarkable for Sykes' monkeys, which are predominantly arboreal (Emerson *et al.* 2011). Therefore, they avoid lower sections of the tree simply due to habitat use, and not necessarily perceived predation risk. However, in the study by Emerson *et al.* (2011), the highest measurements recorded were not on the very top of the canopies as they were in this study. Therefore, perhaps if Emerson *et al.* (2011) had added another patch at the very top of the tree canopy, Sykes' monkeys would also find this area more dangerous than lower in the canopy, due to the potential of aerial attack (Makin *et al.* 2012).

As with Makin *et al.* (2012), Emerson *et al.* (2011) did not add in any horizontal patches within the tree canopy, as I have done with this study. Contrary to expectations, the vervets regarded the edge of the tree canopy the least safe zone within the tree. I expected that due to decreased domains of danger (i.e. area where any point is closer to the focal individual than any other individual; Hamilton 1971), this patch would have been considered safer than the top of the tree canopy. Yet, it was considered the most dangerous within the tree patches. It could be that being far out on the side of the canopy reduces the vervets escape options. When an individual is on the edge of a tree there are three options when it comes to escape, either jump to another tree, fall to the ground, or retreat back into the central canopy. Within my experiment, the patch on the edge of the canopy was always on the side of the open grassland. Therefore at this edge patch there were no other trees for the vervets to jump to and escape predation. Thus

they are left with the only options: descend directly to the ground, or retreat back into the central canopy of the tree.

When under the risk of predation, be it from aerial or terrestrial danger, the ground is considered riskier than the trees. This is clear from this experiment as all patches on the ground were used less than any of the tree patches. Therefore, jumping to the ground is less likely to occur when trying to avoid a nearby predator. Therefore, the vervets on the edge of the canopy can only escape predation by retreating back into the canopy. Only having one escape option may make the vervets movements predictable for predators, which would then increase their risk of attack. For this reason, the vervets may not like to spend an extended time foraging in this area. Thus, this is the patch within the tree canopy that is considered most dangerous. In addition to patch 1 opposing predictions for the baseline, vervets did not utilise this patch as predicted when the mobbing call came from the ground (see section 4.3.2 below).

Following Makin *et al.* (2012), I found that the vervets considered the patches underneath the canopy (patches 3, 4 and 5) as relatively safe. This is likely because the vervets have cover from the tree canopy, reducing detection by eagles. Additionally, when they are on the ground, they are close enough to escape into the upper tree canopy in the case of a terrestrial predator attack. As with Makin *et al.* (2012), the vervets considered the grassland patches less safe the further away from the tree they ventured. The open grassland exposed the vervets to both terrestrial and aerial predator attack. The trees provided protection from these threats. Thus, the further away from the tree line the vervets ventured, the less safe they felt. Ultimately, this baseline landscape of fear is how the vervets utilized their landscape on a day-to-day basis. It illustrated how vervets perceived their environment when there was no obvious sign of danger. However, once I manipulated perceived predation risk by using playbacks of alarm calls, the vervets' landscape of fear changed.

## 4.2 Vervet Alarm Calls

### 4.2.1 Terrestrial Predator Alarm Call

When the vervets heard the terrestrial predator alarm call, they changed their foraging behaviour as expected, following the patterns first described by Seyfarth *et al.* (1980a). They used the upper sections more than the lower sections of the trees and the open grassland less than the baseline. Terrestrial predators attack from the ground, therefore when vervets alarm for a terrestrial predator the safest area is up the tree. Consequently, their movements to the upper sections of the tree are likely an effort to reduce the risk of attack. The lower sections are still used, but less intensely. Out in the open they are vulnerable to a terrestrial predator attack, so not surprisingly they reduced their use of areas away from the safety of the trees.

### 4.2.2 Aerial Predator Alarm Call

When the vervets heard the aerial predator alarm call, they shifted their foraging intensity to areas of the landscape less exposed to the sky. This followed the patterns first described by Seyfarth *et al.* (1980a). The canopy provides a degree of cover and thus a greater degree of safety from aerial predators (Seyfarth *et al.* 1980a). Aerial predators, such as crowned eagles, are visual hunters, locating their potential prey through sight (Liversidge 1991). If the vervets avoid detection, it is likely that they will avoid predation. Thus, in response to perceived predation risk from an aerial predator, they avoided the more exposed tops of the trees and the open grassland. They avoided the base of the tree, patch 5, similarly to the tops of the trees. Although the canopy covers this patch, it is possible that the vervets avoided it because aerial predators could still see the vervets at this patch, and thus potentially swoop down and take them.

Ultimately, the GUDs recorded that the vervets reacted to both the terrestrial and aerial predator alarm calls in manners similar to the behavioural observations of Seyfarth *et al.* (1980b). As a result, this suggests that the vervets recognised these calls in a functionally referential manner, as found previously by Seyfarth *et al.* (1980b).

Moreover, the GUDs provided quantifiable measures of the vervets' perceived predation risk when I manipulated risk across the landscape using the playbacks.

### 4.3 Eavesdropping

#### 4.3.1 Red-backed Shrike Alarm Call

Contrary to expectations, the vervets did not alter their foraging behaviour in response to the red-backed shrike alarm call (i.e. there was no significant difference between the baseline landscape of fear and when the red-backed shrike's alarm was played). It is possible that when the vervets heard the red-backed shrike's alarm they increased their vigilance. However, being a small passerine bird the red-backed shrike alarm calls for a number potential predators (Liversidge 1991), many of which would not be a threat to vervets. These could include a multitude of raptors, terrestrial predators, or unknown objects (Liversidge 1991). As the red-backed shrike's call is quite broad, it is possible that the vervets did not consider it as a reliable source (i.e. honest signal) of real threats. Thus, the degree to which they responded (e.g. potential increase in vigilance) was not enough to significantly change their feeding effort across the different patches. Moreover, as shrike's alarm call lacks a referential aspect, the vervets would not know the location of the potential threat by eavesdropping. As a result, they would not know where to move within the landscape to reduce predation risk. Thus, they may have remained at a patch until they obtained additional information (e.g. visual sighting or vervet alarm call) of the location of the potential predator.

In contrast, another potential explanation could be that as they did not adjust their spatial use of the landscape in reaction to the call, it may be that they simply do not associate the red-backed shrike's call with increased predation risk. If this is the case, then it may still be possible that they do eavesdrop on the alarm calls of other bird species. Thus, I suggest further research into this possibility, using a broader range of bird species which may generate different results.

#### 4.3.2 Mobbing Calls

The vervets shifted their landscape of fear in response to the mixed-species bird mobbing call played from two separate locations. This call was not functionally referential, in that it did not encode a particular predator type. Nor was it urgency-based, as it did not change regarding the degree of the threat. It was simply a flock of mixed bird species mobbing a potential predator, and thus only gave insight into predator presence and its potential location. However, the way in which the vervets responded to these treatments suggests that they interpreted the calls in a referential manner, by using the location of the call to grasp additional information regarding the threat.

When I played the mobbing call from the ground (simulating the mobbing of a terrestrial predator), the vervets responded as if a terrestrial predator alarm call had been given. They shifted their foraging so that they fed less on the ground and more within the trees. When I played the mobbing call from up in the trees (stimulating an aerial predator being mobbed), the vervets responded as if they had heard the aerial predator alarm call. They avoided patches exposed to the sky and concentrated their feeding under the tree canopy.

The only variation in patch use between the two mobbing calls and the vervet alarm calls was between the terrestrial vervet alarm call and mobbing call from the ground. This difference however, was only evident in the patch on the edge of the tree canopy (patch 1, Fig. 6). Contrary to expectations, the vervets considered this patch as the most dangerous patch within the tree. When I played the mobbing call from the ground, I expected the vervets would use this patch more as it is up off the ground, yet they used it significantly less than during the terrestrial predator call.

A possible explanation of this could be the compounding impact of two factors: 1) since this was a generalised mobbing call, the vervets have incomplete information regarding the threat, and 2) they have limited escape options at this patch, making it riskier to forage there. Mobbing calls could indicate a variety of predators, from small domestic cats, to leopards, domestic dogs, or even snakes. The information transmitted in these calls to the vervets is hence unclear. The only information that the vervets can grasp is that there is a potential threat, and it is found on the ground. Due to the uncertainty of this information, the vervets may have decided to be cautious in patch 1.

The vervets already consider patch 1 as the most dangerous patch in the tree (see baseline pattern above), which is likely due to the limited escape options from this area (see section 4.1). Therefore, the combination of these two factors may have caused patch 1 to be used less during the mobbing call from the ground treatment.

The meaning of an alarm call can change when the locality of the predator changes (Fichtel and Kappeler 2002), which is what I found when I played the same mobbing call to the vervets from different locations. When the vervets heard the mobbing calls, they took note of the location, and associated this with a predators generally found in these areas (as indicated by their feeding effort). Thus, they seem to use this information in a referential manner. A referential manner implies that listeners relate a specific meaning to a vocalization without a context, such as a predator type. In the case of the mobbing calls, the vervets heard the call and needed no other contextual cues, such as the birds mobbing, or a visual predator cue, to respond.

For example, meerkats have three main functionally referential alarm calls which are acoustically distinct (Manser 2001). One for terrestrial predators, one for aerial predators, and one which calls for group aggregation (Manser 2001). When these calls are sounded, the meerkats need no other information to respond appropriately to the signal, indicating that the calls are functionally referential (Manser 2001; Manser *et al.* 2001). The vervet monkeys in this study responded similarly to the mixed-species mobbing calls, yet instead of acoustically different signals, the vervets grasped additional information from the location of the call, and responded in accordance with this information. To my knowledge, the skill of understanding eavesdropped calls in a referential manner is unique to primates, and is still highly under-quantified. Moreover, this is the first study to quantify this ability using GUDs.

Seyfarth and Cheney (1990) found a similar situation with vervet monkeys eavesdropping on the superb starling alarm call. This small passerine bird has two distinct alarm call types, which denote specific escape responses (Seyfarth and Cheney 1990). The superb starling gives distinct alarm calls for terrestrial and aerial threats (Hauser 1988; Cheney and Seyfarth 1990). However, these alarms are not alarms for specific predator classes, as vervet alarms are, instead they denote the location of the threat (Seyfarth and Cheney 1990). For instance, if a superb starling noticed a raptor on

the ground, they called the terrestrial alarm, and not the aerial alarm (Seyfarth and Cheney 1990). Seyfarth and Cheney (1990) found that the vervets responded to these two alarms in the same manner as they responded to their own aerial and terrestrial predator alarms. Therefore, the vervets were gathering information regarding the location of the predator, and not the predator class. I believe my results provide similar findings with the mobbing call treatments played from different locations.

In order to respond to an eavesdropped signal in a manner that benefits them, the vervets would have to provide referential meaning to any calls they use. This is because vervets have to deal with varied predator threats, which results in several mutually exclusive responses to predators (Seyfarth *et al.* 1980a). For instance, if the vervets responded as if an eagle was about, it is likely that they would move away from the tops of the trees, yet this move may make them more vulnerable to attack from terrestrial predators. Therefore, vervets need to know the type of predator in order to perform the correct escape response. My results suggest that the locations of the mobbing call allowed the vervets to determine this, and hence escape appropriately. Additionally, the mobbing calls played were identical, and only the location shifted between treatments. The vervets were able to perceive that the mobbing call location changed. They were therefore able to apply referential meaning to these non-referential calls in an effort to use them to their greatest advantage.

Ultimately, vervet monkeys likely consider a mixed-species flock mobbing call an honest signal. Generally, single individuals with selfish motives can give dishonest signals (Dawkins and Guilford 1991). For example, single dominant great tits gave false alarm calls to steal food from other dominant conspecifics (Møller 1988). However, in the case of a mobbing call, many heterospecifics birds give these calls, with the common goal of driving a predator off (Marler 2005; Randler and Förschler 2011). The possibility of these heterospecifics dishonestly mobbing, for a common selfish goal, is unlikely. Therefore, these mobbing signals are likely honest signals (Lind *et al.* 2005). Moreover, as many individuals are calling the mobbing calls likely provide physically stronger signal, which may emphasize the urgency of the situation. The combination of these points could therefore be a strong motivation for the vervets to respond to these calls.

#### 4.4 Total feeding effort

Among all the treatments that shifted the pattern of foraging, only the playbacks of an aerial predator and mobbing from up the tree caused the vervets to reduce the overall feeding effort (i.e. achieve high GUDs) across the landscape. Although the vervets felt an increased fear from the terrestrial predator alarm, and mobbing call from the ground, they ate the same amount of food as when no alarm calls were given. Thus, the only difference between these treatments is that they changed their pattern of patch use, with greater feeding effort shifted to perceived safer patches.

In contrast, the aerial predator alarm call and mobbing call from up the tree caused the vervets to eat less food overall. The only patches where feeding effort increased were under the canopy of the tree (patch 3) and a meter off the ground (patch 4). All other patches were used less than the baseline. Ultimately, the lower overall feeding effort across the landscape indicates that vervets reduce feeding and spend more time in anti-predator behaviour (e.g. increased vigilance). Thus, as these two calls elicited the greatest response, this suggests that aerial predators likely constrain foraging and location options more for vervet monkeys than terrestrial predators. This is in accordance with the findings of Willems and Hill (2009).

The location of the study site may compound this effect. The sites I used, although in natural vegetation, are on the periphery of suburban areas, therefore large terrestrial predators such as leopard or caracal are scarce. However, the vervets do have to contend with other terrestrial predators such as domestic dogs, and black-backed jackal. Yet the predation risk from terrestrial predators is likely less in sub-urban areas than in more untransformed regions. In contrast, crowned eagles are found in relatively large numbers in sub-urban landscapes around Pietermaritzburg (S. McPherson 2013, pers. comm.). As a result, it is likely that the threat from aerial predators is higher than that from terrestrial predators in my study region.

This however, may not be far from the conditions in more natural environments. Willems and Hill (2009) researched vervets in the Soutspansberg mountain range in South Africa, and found that the vervets encountered and alarmed most for aerial predators (72% of all identified alarms), and much less for terrestrial predators (5%), indicating the increased threat from aerial predators.



Finally, the vervets did not react differently to both the mobbing call from up in the tree and the eagle's alarm call. This is indicated by the similarity in landscape use and the total amount of food eaten in both of these treatments. Additionally, the intensities of foraging during the mobbing call from the ground and terrestrial alarm call were similar. This suggests that the vervets responded to the eavesdropped calls as intensely as they responded to their own species' alarms. This is similar to Zuberbühler *et al.* (1999b) and Zuberbühler (2000a) who found that Diana Monkeys respond similarly to the eavesdropped species-specific alarm calls of Campbell's monkeys as they do to their own species-specific alarm calls.

There are two potential explanations for these results. Either, the vervets view both types of signals as effective warning signals of predators, and therefore respond equally. Alternatively, mobbing calls provide limited information to the vervets, resulting in the vervets being over-cautious, and hence responding to this signal in similar proportion to their own predator alarms. Moreover, they likely obtain enough information from the location of the mobbing call to grasp an understanding of the potential type of threat. This results in them responding to a mobbing call in an over-cautious manner with a specific escape strategy. Schmidt *et al.* (2008) found a similar situation in eastern chipmunks. They found that the eastern chipmunk eavesdrops on the alarm calls of the eastern tufted titmouse, as well as mixed-species flock mobbing calls. However, the chipmunks' response to the mobbing calls was greater than the titmouse calls because the mobbing calls only provided limited information on a potential threat. Schmidt *et al.* (2008) suggested that this was because the chipmunks were being over-cautious. Similarly, it is possible that the vervets responded to the mobbing calls in the same degree as to their own predator calls due to over-caution in the face of limited information.

#### 4.5 Conclusions

Ultimately, the vervet monkeys perceived predation risk within their environment, and because of this, they foraged differently across the landscape. Their baseline landscape of fear indicated that they feed more intensively in the trees compared to the open

grassland. The vervets shifted their landscape of fear appropriately when exposed to vervet terrestrial and aerial predator alarm calls. Additionally, the vervets went beyond the knowledge of their own alarm calls by eavesdropping. They shifted their landscape use in response to mobbing calls from two different locations. The vervets took note of where the call came from, and responded in accordance with the call location. This response suggests that the vervets understood a non-functionally referential alarm call (such as a mobbing call), coupled this with information regarding the location of the call, and interpreted it in a referential manner. Ultimately, the results of my study indicate that vervets do not solely rely on their own vigilance to reduce predation risk, but rather also incorporate social information via eavesdropping. Moreover, they are able to obtain referential information from these eavesdropped signals which likely greatly improves their survival and fitness.

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