ENVIRONMENTAL EFFECTS ON GROUP STRUCTURE AND VIGILANCE IN VERVET MONKEYS

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Abstract

Narrow riparian woodlands along non-perennial streams have made it possible for vervet monkeys to penetrate the semi-arid karoo ecosystem of South Africa, while artificial water points have more recently allowed these populations to colonize much more marginal habitat away from natural water sources. In order to determine the sequelae of life in these narrow, linear woodlands for historically 'natural' populations, I determined the size of troops in relation to their reliance on natural and artificial water sources and collected detailed data from two river-centred troops on activity, diet and ranging behaviour over an annual cycle. These data indicate that river-centred troops were distinctive primarily for their large group sizes and, consequently, their large adult cohorts, and the extent of home range overlap in what is regarded as a territorial species. While large group size carried the corollary of increased day journey length and longer estimated interbirth intervals, there was little other indication of ecological stress. Specifically, the rate of predation appears to be lower than observed at other sites. Predation encounters here, encourage the use of predator vigilance rather than influencing the use of space within the habitat. The high density of Acacia karoo, which accounted for a third of annual foraging effort in what was a relatively depauperate floristic habitat, allows for an adequate energy intake for groups of this size. I ascribed the large group size and home range overlap to the inability of groups to undergo fission.

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Gregariousness in cattle and men. Francis Galton, 1871

CHAPTER ONE

Introduction

1.1 Group Structure

Models that derive the limits of group size from the constraining effects of environmental variables on activity schedules have been very successful in predicting the distribution of social primates (Dunbar, 1996; Korstjens, Verhoeckx, Dunbar, 2006). Such modeling has value, not only for recreating a species' evolutionary biogeography, but also for simulating the future consequences of climate change. Nevertheless, by necessity, they operate at a relatively coarse spatial scale and are not necessarily able to discern local presence or absence. A very good example of this is the failure of a recent activity budget model to detect the presence of vervet monkeys (*Cercopithecus aethiops* L.) in the semi-arid karoo of South Africa (Figure 5 in Willems & Hill, 2009a), whereas they have had a historically documented presence since at least the eighteenth century (Skead, 1987) and are now regionally abundant.

Vervets, after savanna baboons (*Papio hamadryas* L.), are the most widely distributed non-human African primate (Wolfheim, 1983). Despite this biogeographical breadth, however, they avoid both high forest and open habitats, preferring closed riparian woodland (Enstam & Isbell, 2007). While the provision of artificial point water sources for livestock has increased their distribution dramatically, this is certainly the case in the karoo, where local historical populations have been confined to narrow strips of *Acacia karroo* (Heyne) woodland along non-perennial rivers and streams in otherwise inhospitable open country. Clearly, then, the failure of the activity budget model to predict their presence is a consequence of the fact that these woodlands are, in effect, anomalous features in the larger landscape. Nevertheless, they are very important components of the local ecosystem, both as refugia and corridors (Puth & Wilson, 2001), especially in the face of increasing temperatures and decreasing rainfall in this part of South Africa (Hoffman, Carrick, Gillson, & West, 2009). I am interested in highlighting the demographic and ecological characteristics of such a population, with an emphasis on the impact of predation, in order to identify the features that have shaped it.

1.2.1 Predation

The ability to avoid injury or death from predators is one of the most important aspects of an organism's behaviour. Group living has long been thought to be driven by predation risk (Hill & Dunbar, 1998; Pulliam, 1973; van Schaik, 1983; but see Wrangham, 1980). Non-human primates, and more specifically, vervet monkeys, the subject of this study, employ a wide variety of anti-predator behaviours ranging from mobbing behaviour (Baldellou & Henzi, 1992) and alarm calling (Struhsaker, 1967a; Seyfarth, Cheney & Marler, 1980) to increasing vigilance in predator rich environments (Jaffe & Isbell, 2009). Additionally, the risk of predation can influence factors such as space use - whereby areas with a high perceived risk of predation are avoided- (Willems & Hill, 2009b), parenting strategies -in the form of mothers increasing vigilance when separated from infants- (Treves, Drescher, & Snowdon, 2003) and intra-group relations, through decreasing the amount of distance between individuals (Rose & Fedigan, 1995; Watts, 1998).

Here, I examine some of the previous work that has focused on the environmental and social factors influencing anti-predator behaviour before I identify my research aims.

1.2.2 Predation Risk vs Predation Rate: A note on terminology

The role of predation and its effects on group composition and behaviour has received a great deal of attention and in some cases generated conflicting results. For example, Anderson (1986) reported that there is a positive correlation between predation *rate* and group size in many species of primates, while Isbell (1994) found a negative relationship. Alternatively, Hill and Lee (1998) found a positive relationship between group size and predation *risk* across 39 primate species. One reason for these contradictory results is that most studies fail to recognize the importance of distinguishing between predation risk and predation rate (Hill & Dunbar, 1998; Vermeij, 1982). Hill and Dunbar (1998) defined predation rate as the annual mortality within a population that is attributable to predation and it represents the level of successful predator attacks that animals are unable to control after they have implemented their anti-predator strategies. Predation risk, on the other hand, is the animals' own perception of the likelihood of being subject to an attack by a predator, regardless of whether the attack is successful or not. An understanding of the role of predation as a selective pressure on primates can be achieved through attempts to study the factors that are important in determining a primate's perceived risk of predation (Hill & Dunbar, 1998).

1.3.1 Vigilance

Diurnal non-human primates have to cope with three main types of predators: raptors, felids and poisonous or constricting snakes (van Schaik & van Noordwijk, 1989). The success rate of these predators is greatly reduced if the prey detects the predator prior to an attack. An animal monitoring its surroundings outside its immediate vicinity is referred to as vigilance behaviour. Vigilance behaviour then is assumed to be a potentially successful way of avoiding a predator (van Schaik & van Noordwijk, 1989) and may express an animal's perceived risk of predation (Treves, et al., 2003; Welp, Rushen, Kramer, Festa-Bianchet & de Passille, 2004). Understanding the determinants of vigilance behaviour, and what drives the time trade-offs associated with vigilance, is important for determining how social and ecological pressures shape group size and structure (Hirsch, 2002).

1.3.2 Types of vigilance

Vigilance can serve multiple functions beyond that of detecting predators. Social vigilance is used to monitor the actions of conspecifics within a group. In primates, social vigilance has been shown to be a technique to detect potential competitors (Balldelou & Henzi, 1992), mates (Bercovitch, 1988) as well as potential infanticide attacks (Cowlishaw, 1994; Cowlishaw, 1998). Treves (2000) review on vigilance behaviour found that most studies on primates do not exclude social vigilance, both reflecting a mistaken assumption about predator detection strategies and highlighting the need for further, appropriately designed examinations.

1.4 Factors affecting levels of vigilance

1.4.1 Predation events

Predation rate is difficult to study in primates as predation attempts are rarely observed (Isbell, 1994). Isbell and Young (1993a) suggest that this is a result of the overall rate of predation in primate populations being relatively low. Extreme rates of predation have been known to be the source of change among social groups. Jaffe and

Isbell (2009) report a predator-induced group fusion event with two vervet troops following a period of extreme leopard predation. In addition, they noted changes in ranging and agonistic behaviour following this fusion event.

What is yet to be determined is the influence a predator encounter has on the vigilance behaviour of an individual. The level of vigilance, at least in humans, is known to be positively correlated with anxiety (Broadbent & Broadbent, 1988). Given that a predator sighting or an attack is a moment of extreme anxiety, the level of individual vigilance should increase following such an event preventing further attack from the same predator. At the same time, however, vigilance is argued to take time away from other activities such as foraging and resting and therefore comes at a cost (Cowlishaw, 1998; Lima, 1992). It is predicted, then, that following a predator sighting or attack, individual levels of vigilance should, at some point, return to baseline levels. The time at which it takes to return to baseline may be affected by the predator class, vegetation density and severity of the attack and may therefore provide some indication of levels of perceived risk.

1.4.2 Group Size

In theory, one of the main benefits of group living is the sharing of vigilance among group members (Treves, 1998; van Schaik & van Hooff, 1983). The ability to detect the presence or approach of a predator should improve with increasing group size (van Schaik & van Noordwijk, 1989). One of the predictions of this theory has been rigorously tested and deserves to be highlighted. That is, if the detection of a predator improves with group size, and vigilance is assumed to come at a cost (Pulliam, 1973; van

Schaik & van Noordwijk, 1989), then individual vigilance levels should decrease with increasing group size**.** This trend has been observed in well over 50 species of birds and mammals (Edgar, 1989). Of interest however, are the more recent studies reporting the absence of this effect in primates (Cowlishaw, 1998; Rose and Fedigan, 1995; Treves, 1998). Although Isbell and Young (1993b) found a negative correlation in vervets, they failed to remove the effects of sex and dominance rank from their analysis. Treves (2000) provides a functional explanation as to why primate vigilance behaviour does not follow the expected trend. Primates face a unique challenge in balancing within-group vigilance with anti-predator vigilance, because they have narrow visual fields and face severe threats from conspecifics. And although the risk that a given individual is killed during a successful attack declines with increasing group size, when a group contains a mix of species, sexes, age classes or safe and vulnerable individuals, group size does not adequately measure individual risk.

1.4.3 Sex

Males and females face varying levels of risks associated with each predator class. Females are predicted to be more sensitive to the risk of predation as their smaller size makes them more vulnerable (Cowlishaw, 1998). Yet this has not been observed in several primate species. In white-headed capuchins (*Cebus albifrons)*(Rose & Fedigan, 1995), vervets (Baldellou & Henzi, 1992), white-tufted capuchins (*Cebus apella)* (van Schaik & van Noordwijk, 1989) and Thomas's langurs (*Presbytis thomasi*) (Steenbeek, Piek, van Buul & van Hooff, 1999), males were more vigilant than females. However, if males are shown to provide an anti-predator detection service for females, then perhaps females need not spend more time vigilant than males. van Schaik & van Noordwijk

(1989) and Baldellou and Henzi (1992) found that male capuchin and vervet monkeys do not provide such a service as their increased vigilance actually serves their own reproductive interests. This is in contrast to females prioritizing vigilance for survival strategies (Cowlishaw, 1998). Regardless of focus, females may still obtain benefits from male vigilance, both from their incidental detection of predators as well as, in the case of baboons, their detection of potentially infanticidal males outside the group (Cowlishaw, 1998).

1.4.4 Environment

An individual's perceived risk of predation has a number of different components, many of which are closely related to the local environment (Hill & Dunbar, 1998). Willems & Hill (2009b) demonstrated that vervet monkey ranging behaviour is not based solely on the location of resources. Instead, vervets balance the trade-offs between maintaining an adequate energy intake and reducing the overall risk of predation by avoiding areas perceived to be rich in predators. Baboons (*Papio cynocephalus ursinus)* have been observed to forage, travel, rest and groom in safer habitats more often than in areas which are perceived as having a higher risk of predation (Cowlishaw, 1997). These studies show that some primates are acutely aware of the varying risk of predation inside their habitat and can adjust their ranging behaviour accordingly (Hill & Dunbar, 1998).

1.4.5 Micro-habitat

Along with its effect on the use of space, perceived predation risk can be seen to influence anti-predator behaviour with respect to the location of an individual within its environment. Hamilton (1971) suggested that individuals on the periphery of a group should have a higher risk of predation than those in the center. If the risk of predation is higher, then individuals on the periphery of the group are predicted to spend a greater proportion of their time vigilant. van Schaik and van Noordwijk (1989) found that male capuchin monkeys were more vigilant than females because they spent a greater amount on time on the periphery. If individuals are more at risk on the periphery, then individual predation risk should also be positively correlated with the distance of one's neighbours. Cowlishaw (1998) showed that when individual baboons were spaced further apart, individual vigilance increased. Alternatively, Hirsch (2002) found the opposite effect in brown capuchin monkeys, in which vigilance was negatively correlated with inter-individual distance. The latter study may suggest that vigilance is primarily used for social monitoring or highlights a need to design studies on predation that see the inclusion of both social and predator vigilance. The relationship between vigilance behaviour and location within a group is exaggerated when placed in the context of proximity to predator refugia. Male baboons spend more time vigilant in areas that are distant from such refuges (Cowlishaw, 1998). In contrast, Jaffe and Isbell (2009) found that vervets were less vigilant in open areas. She suggested that open habitat lowers an animal's perceived risk of predation because of the increase in visibility. Given that leopard (*Panthera pardus*) predation is the cause of numerous vervet deaths in her study area, open habitat may decrease the chance of being preyed upon by a leopard thereby reducing the need for vigilance.

The height of an individual in a tree has also received a great deal of attention within studies of primate vigilance. The risk of aerial predation increases as an individual approaches the top of a tree as an animal is more prone to attack. Steenbeek and colleagues (1999) found female Thomas's langurs had an increase in predator induced injuries as they occupied higher positions in trees. However, in environments characterised by low density vegetation, vigilance may prove more effective with increases in height. Steenbeek et al. (1999) found a positive correlation between height and the amount of time spent vigilant in Thomas's langurs only in areas of troop overlap. This may suggests that vigilance in these areas is used to monitor other troops. In contrast, van Schaik & van Noordwijk (1989) found that capuchin monkeys are increasingly vigilant as they move closer to the ground. It was noted that the dense bush surrounding the ground level makes capuchin monkeys more prone to stealth attacks from leopards. These findings suggest that both the classes of predators and local environment play a role in the vigilance behaviour of primates.

1.5 Aims

My general research questions have been directed at the local sustainability of these vervet populations and the consequences of life, for an obligate social mammal, restricted to these narrow riparian strips, where migration pathways are severely constrained (see also Isbell, Cheney & Seyfarth, 2002) and the effects of drought are exacerbated by both high summer temperatures and very low winter ones.

My primary objectives are to first outline the population structure and habitat use of vervet monkeys at a high latitude site in South Africa (Samara Game Reserve, Eastern Cape). From here I will then examine the extent to which the anti-predator behaviour and the empirically determined risk of predation, if any, influence the use of habitat in this population. Vervet monkeys are well suited to research on the effects of predation because both avian and terrestrial predators hunt them and the specificity of their alarm calls. Seyfarth and colleagues (1980) indicates that predation risk has imposed strong selection pressures on this species. The predator guild-specific alarm calls, in addition to the relative ease with which vervet monkeys are habituated allows for collection of highly detailed information on range use, and both anti-predator and social behaviour (Willems & Hill, 2009b) and makes them an ideal species to use in this project.

Most of the above studies conducted on vervets have been restricted to observations gathered on populations in Kenya (Isbell & Jaffe, 2009; Seyfarth, et al, 1980; Strusaker 1967a). In those studies, the troop size was smaller (N=22) than those under examination here (N=60). Troop size is known to implicate an individual's risk of predation (Hamilton, 1971) as well as the chance of detecting an outside threat (Treves, 1998; van Schaik, van Noordwijk, Warsono & Sutriono, 1983). Predator impact studies on vervets have all be conducted in areas with different predator landscapes than the ones found here. In particular, the absence of leopard (*Panthera pardus)* greatly reduces the risk of predation in trees (Struhsaker, 1967; Cowlishaw, 1994). Additionally, there have been no confirmed reports of baboons (*Papio ursinus*) predating on vervets in the Eastern Cape province of South Africa. Therefore, it is reasonable to assume that the vervet population found in Samara game reserve may behave differently within their predator environment.

My broad aims, therefore, are to:

1) Highlight the ecological and demographic characteristics of this population
2) Produce and verify a definition of predator vigilance
3) Survey the social and environmental factors contributing to vigilance

4) Examine behavioural outcomes following a predator encounter

5) Quantify the influence that perceived predation risk has on space use

CHAPTER TWO

Methods

2.1 Study Animal

2.1.1 Habitat and Ecology

The vervet monkey (*Chlorocebus aethiops pygerythrus*) is a semi terrestrial Old World monkey. Next to baboons, vervets are the most widely distributed of the non-human African primates (Struhsaker, 1967a; Wolfheim, 1983). They occur primary in riparian woodland throughout sub-Saharan Africa, ranging from Senegal to Ethiopia and as far south as South Africa (Struhsaker, 1967b). Their wide distribution may be constrained by the presence of water and access to adequate sleeping sites (Wrangham, 1981) and enhanced by their generalist diet. This diet consists of leaves, shoots, seeds, flowers, berries, nuts, fungi, birds, bird eggs, invertebrates and vertebrates (Chapman, Fedigan & Fedigan, 1988; Struhsaker, 1967a; Wrangham & Waterman, 1981).

Vervet monkeys are territorial in periods where food availability is scarce, (Chapman & Fedigan, 1984) and, if necessary will aggressively defend their home ranges (Cheney, 1980). These home ranges can vary in size, from 0.06 km^2 to 1.78 km^2 (Harrison, 1983; Willems & Hill, 2009b). The minimum distance travelled each day can range from 135 m to 2251 m and is a result of home range size, habitat productivity and location of water sources. (Struhsaker, 1967a; Wrangham, 1981).

2.1.2 Social Structure

Vervets live in multi-male, multi-female groups with an average troop size of 25 animals. (Chapman, et al., 1985). Females are philopatric, whereas males leave their natal troops at puberty. Female dominance hierarchies are linear and relatively stable, with rank being inherited (Struhsaker, 1967b). This is in contrast to the males, whose hierarchy may change throughout the year (Cheney & Seyfarth, 1989).

2.1.3 Predators

Due to their small size and the environments they inhabit, vervets are susceptible to predation from many different predators. Avian predators include the crowned eagle (*Stephanoaetus coronatus*), verreaux's eagle (*Aquila verreauxii*) as well as the cape eagle owl (*Bubo capensis*). Although snakes do not actively prey on vervets, with the exception of the rock python (*Python sebae*), they remain a source of extrinsic mortality (Willems & Hill, 2009b). Some of the snake species known to kill vervets include black mamba (*Dendroaspis polylepis*), boomslang (*Dispholidus typhus*), puff adder (*Bitis arietans*) and the Mozambican spitting cobra (*Naja mossambica*) (Seyfarth et al, 1980; Willems & Hill, 2009b). Finally, leopard (*Panthera pardus*), lion (*Panthera leo*) and chacma baboon (*Papio hamadryas ursinus*), are potential land predators of vervets (Seyfarth, et al., 1980).

2.1.4 Anti-Predator Behaviour

Perhaps owning to the extent and nature of predation they experience, vervets utilize several anti-predator behaviours of which the most well-known is their predator guild-specific alarm calling. (Seyfarth, et al., 1980). Each acoustically different alarm call evokes contrasting responses which include scanning the ground following a snake call and running into trees following a leopard call (Seyfarth, et al., 1980). This alarm calling behaviour has been argued to be a result of both kin and individual selection, acting on an individual’s inclusive fitness (Cheney & Seyfarth, 1981). In addition to alarm calling, vervets have been reported to engage in predator mobbing (Baldellou and Henzi, 1992), a process whereby individuals collectively attack or harass a predator.

2.2 Study Site

2.2.1 Location

Data were collected from an ongoing study of a vervet monkey population in the Samara Game Reserve, Eastern Cape Province, South Africa (32° 22’S, 24°52’E. Figure 1a). Samara is one of the largest private reserves in South Africa and is situated 35km east of Graaff-Reinet and approximately 260km north of Port Elizabeth. The reserve lies on the southern portion of the Sneeuberg mountain range encompassing a total land area of 34000ha (Figure 1b). The area originally consisted of grazing farmland until 1997, when it was transformed into a private reserve. The reserve is separated north to south by the non-perennial Melk river drainage system. The study site has no artificial water sources. Such point sources of water have been established away from the river and there are generally vervet groups associated with them.

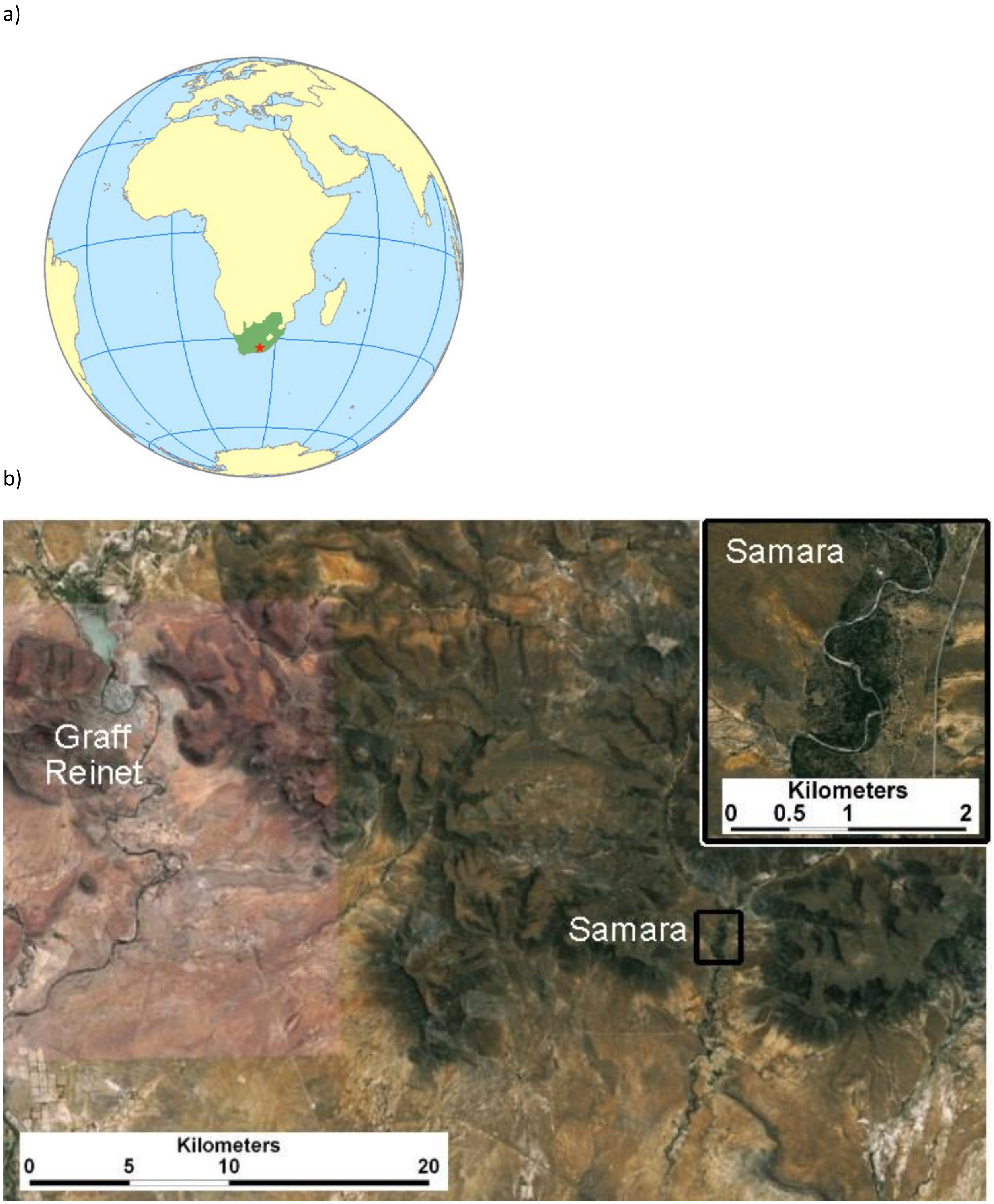


Figure 1. The location of the general study area within South Africa (a) and in relation to the town of Graaff Reinet (b), where the rectangle indicates the study site (enlarged in the inset).

2.2.2 Climate and Seasonality

The Samara game reserve has a semi-arid climate and as a result experiences strong seasonality in rainfall, temperature and day-length. The mean annual rainfall is 330 mm, with most rain falling from November to February (Figure 2, courtesy of the South African Weather Service). The mean annual temperature is 18.6 °C. The monthly mean temperatures are given in Figure 3 (courtesy of the South African Weather Service). The coldest month is July when snow falls on the surrounding mountains (mean minimum 4°C), while December and January are the hottest (mean maximum: 34°C). Day-length peaks in December at 14 hours six minutes and drops to 9 hours 54 minutes in June.

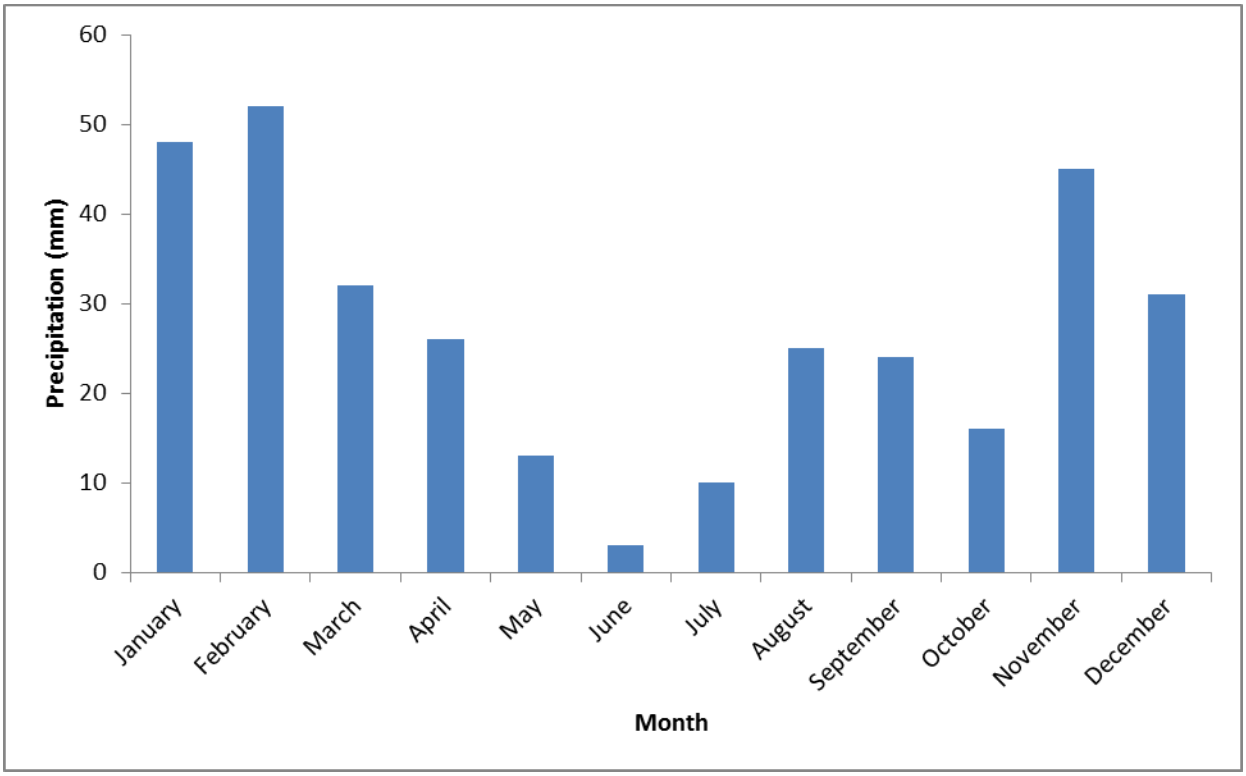


Figure 2. Mean monthly rainfall for the town of Graff-Reinet, 35 km east of Samara Game Reserve.

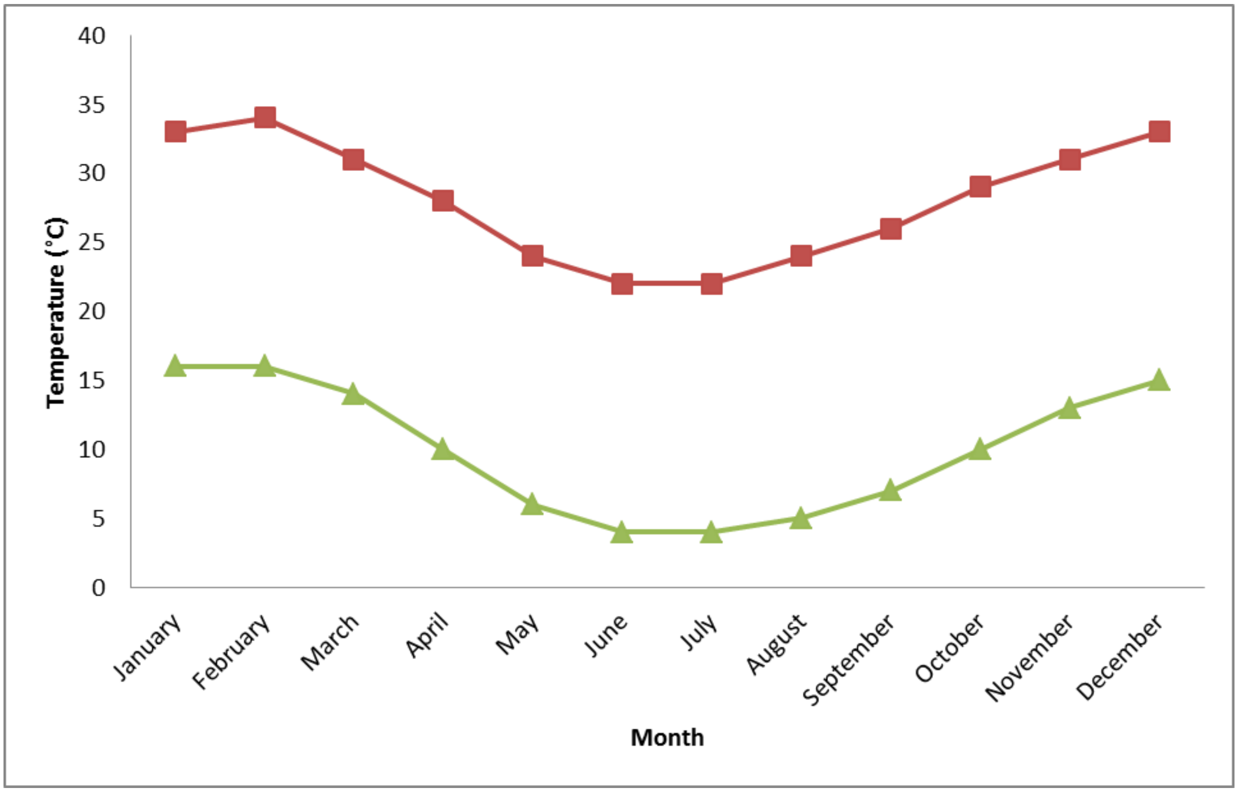


Figure 3. Average maximum and minimum temperatures arranged by month for the town of Graaff-Reinet, 35 km east of Samara Game Reserve.

2.2.3 Flora

The Samara game reserve is made up of four biomes which include: savannah, plateau grasslands, nama karoo and valley bushveld. The woodland adjacent to the riverbed consists primarily of *Acacia karoo*, *Lycium oxycarpum*, *Schinus molle* and *Rhus lancea*. The grasslands found above consist primarily of *Carissa bispinosa*, *Grewia robusta* and *Rhus longispina*.

2.2.4 Fauna

The Samara game reserve has an abundant collection of mammals ranging from large ungulate species such as white rhinoceros (*Ceratotherium simum*), greater kudu (*Tragelaphus strepsiceros*) and gemsbok (*Oryx gazelle*) to medium and small sized ungulates such as springbok (*Antidorcas marsupialis*) or Steenbok (*Raphicerus campestris*). The primates are represented only by two species: chacma baboon and vervet monkey. Samara is home to over 200 avian species, including the verreaux`s eagle (*Aquila verreauxii)*, martial eagle (*Polemaetus bellicosus*), Giant eagle owl (*Bubo lacteus*) and Cape eagle owl (*Bubo capensis*), all of which are potential predators of vervets A land predator community consists of caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*) and black-backed jackal (*Canis mesomelas*) as well as potentially dangerous snake species such as boomslang (*Dispholidus typus*), puff adder (*Bitis arietans*), ring-necked spitting cobra (*Hemachatus haemachatus*) and cape cobra (*Naja nivea*).

2.3 Study Population

From February 2010 -November 2011 behavioural data were collected from two free ranging troops. Riverbend Mob (RBM) and Riverside Troop (RST) were habituated in the fall of 2008 and have been under continuous observation since. These two troops occupy adjacent territories, and both came into contact with up to five other neighbouring troops. RST is the larger of the two troops, with larger male, female and non-adult cohorts (Table 1).

Table 1. Group composition and sex ratio for RBM and RST.

	RBM	RST
Males	9	14
Females	18	26
Non-adults	22	32
Group Size	49	72
Sex Ratio (M:F)	0.5	0.54

2.4 Data Collection

2.4.1 Troop Counts

Troops were counted simultaneously by two or more observers during 2009 and 2010, either from vehicles or on foot at distances of 10-100m. All troops were counted at least twice and their locations identified with a GPS. Most troops were located early in the mornings at their sleeping sites and counted as they departed. This allowed us to obtain repeated, reliable counts of smaller troops in open-country away from the river. Counts of troops with home ranges centred on the river were made as they crossed roads or dry river beds. Apart from the two study troops, for which exact troop size records were kept, counts of such troops are best regarded as conservative estimates of troop size.

2.4.2 Behavioural Observations

RBM and RST were followed ten hours a day for a minimum of 8 days per month (Table 2). During the austral winter, data collection began at 7:00 am and finished at 5:00 pm. During the austral summer, data collection began either at 5:00 am or 8:30 am and finished at 3:00 pm or 6:30 pm respectively. This schedule was necessitated by the change in photoperiod during the course of the year.

Table 2. Number of observation days and scans per troop.

Month	Observation Days	RBM Observation Days	RBM Scans	RST Observation Days	RST Scans
February	13	8	242	9	697
March	24	21	2573	23	3613
April	20	18	2982	19	4044
May	24	21	3738	22	3927
June	21	20	2694	20	2741
July	19	15	2136	18	3119
August	20	16	1510	16	2061
September	14	9	1020	10	903
October	16	8	1515	8	1415
November	12	9	733	10	1397

Behavioural observations were collected by point scan sampling (Altmann, 1974) at 15 minute intervals. Each scan lasted five minutes, during which data were collected on as many animals as possible. Scans were collected using handheld loggers loaded with Pendragon Forms 5.1 Software. Scan sampling was used to collect data on activity, diet, thermoregulation and other aspects of behaviour (N_{2010}=36898 records) (Table 2). The majority of these scans were collected by myself, and a field assistant, R. Boner. The remainder of the scans were collected by four other students working on other projects. To test for inter-observer reliability R. Boner and I simultaneously carried out a full day of scans on the same troop. Scan data were the same for 99 out of 100 data points.

Table 3. Information collected during a scan sample.

Category	Definition
Time interval	Time when scan was started during the fifteen minute
Identity	Identity of individual
Location	
Ground	Within two meters of the base of a tree, shrub, or cliff
Open	Greater than two meters from the base of a tree, shrub, or cliff
Tree	Plant species, greater than 1.5 meters in height, with secondary structures supported clear off the ground
Shrub	Plant species, greater than 1.5 meters in height, with multiple stems or secondary structures resting on the ground.
Height	Distance of individual from ground e.g. Ground, <1 m, 1-3 m, >3 m
Activity	
Foraging	Gathering, processing or ingesting a food source. Food species and part of plant also recorded.
Moving occurring	Movement greater than one body length without foraging
Allo-groomer	Grooming individual (i.d. of partner)
Allo-receiver	Grooming recipient (i.d. of partner)

Autogroom	Grooming self
Other Social	Playing; copulating
Resting	Neither feeding, socialising or moving.
Aggression	Fight; chase; threaten (i.d. of participants)
Nearest Neighbours	Identity of nearest adult female and male
Nearest Neighbours distance	Distance of individual to neighbour e.g. 0 m, 1 m, 2 m, 3 m, 5 m, 10 m, 15 m, 20 m, >25 m

Posture

Sit	Rest position supported by buttocks and front limbs with slight incline of torso
Stand	The animal is supported by all four limbs and dorsal axis is parallel to the ground
Lay	The animal is not supported by either set of limbs and torso is in contact with ground
Crouching/Hunched	Rest position supported by buttocks. All limbs in contact and held against torso
Chest out	Rest position supported by buttocks. Torso forming an obtuse angle with lower limbs. Back is arched with limbs not covering chest from external environment
Recline	Rest position support by buttocks. Dorsal axis is perpendicular to ground, limbs not covering chest from external environment.

Shade

Yes	Over 50 percent of the animal is out of direct sunlight
No	Over 50 percent of the animal is in direct sunlight
Not applicable	Direct sunlight is not available due to clouds, mountains or time of day

Vigilant

Predator	Resting but alert, or interruption of another activity such as foraging to scan the environment to look at something other than vegetation and conspecifics.
Social	The interruption of another activity or resting to scan the environment in the direction of conspecifics.
Unknown vigilance	Animal displaying both predator and social definitions of
Not Vigilant	Animal does not appear to be alert. This may include resting with eyes closed or uninterrupted foraging

2.4.3 Group Position

RST and RBM's position within their respective home ranges was collected using Garmin Handheld GPS data loggers. The center of the troop was located and a GPS waypoint collected at the start of every 15 minute scan period. These readings, together with data from September 2009 through December 2010, covered 295 full days and were used to derive both day journey lengths and, subsequently, home range areas for each of the two troops. After importing all relevant GPS data, I derived day journey length and travel velocities using both the ET GeoWizards tool (Tchoukanski, 2010) and ArcGIS. We applied the Home Range Tools (HRT) for ArcGIS (Rodgers, et al., 2007) to determine the minimum convex polygon (MCP) estimates of both the home range size (99% MCP) and each troop's core area (50% MCP), using an adaptive kernel with a bandwidth of 25m. Home range overlaps were calculated from GPS readings taken of the location of all other troops when these were observed in areas used by the two study troops. An aerial photograph allowed us to extract all trees and shrubs in the field site to determine distances of vervets to trees and shrubs.

2.4.4 Body Mass

I obtained body mass data from adults of both sexes that were anaesthetized for the surgical implantation of temperature loggers (Wits Animal Ethics Screening Committee - Clearance Number 2010/41/04).

2.4.5 Statistical analysis

The mixed model on factors affecting the use of vigilance was conducted by Dr. Parry Clarke using the R statistical software (R Foundation for Statistical Computing, 2011). All remaining tests were conducted with the JMP 9 statistical package (SAS Institute, 2007), with alpha set at 0.05.

2.5.6 Vegetation Surveys

The study site was stratified into physiognomic–physiographic units using a 1:12,000 aerial photograph and located 35 sample plots (400m^2) on a randomly stratified basis within the various identified units. Braun-Blanquet vegetation and habitat surveys were conducted in each of the sample plots during March 2010 to define plant communities (Kent and Coker 2008). All plant species in each of the plots were recorded and the percentage cover was estimated for the tree, shrub, and herbaceous layers using the modified 9-degree Braun-Blanquet sampling scale (Kent & Coker 2008). The floristic data were analyzed using the Weighted Two-Way Indicator Species Analysis, TWINSPAN (Tichý et al. 2007) to obtain a first approximation of the main plant communities. The classification was then refined by applying Braun-Blanquet procedures (Brown and Bredenkamp 1994).

2.5.7 Ad Libitum Data Collection

The GPS position of the monkeys was taken when at least one individual monkey made a predator vocalization. When possible, the identity of the predator was noted, as well as the number of individuals that responded with alarm calls and the reaction to these predator calls (Figure 4). Due to the unhabituated nature of the predators, there were instances in which the observer could not visibly identify the predator. Willems & Hill (2009b) argue that even though some alarm responses do not equate to the actual presence of a predator they still express the monkeys' perception of predator-specific risk and are therefore equally informative. I also recorded whenever an individual supplanted or displaced another individual in order to be able to construct dominance hierarchies. These dominance hierarchies were generated using De Vries, Stevens and Vervaecke (2006) modified version of David's score (David, 1988). This technique corrects for the number of interactions recorded within each dyad. I recorded the location of inter-troop encounters as well as their duration, the number and sex of participants and their contexts (e.g. competition over a water source). In addition to these behavioral data, records have been kept of all births, deaths and migration events since November 2008.

Figure 4. Vervets occupying the top portion of a shrub during an encounter with a jackal.

2.6 Data Analysis

2.6.1 Angle and speed of travel

When possible, I calculated the angle at which either troop was heading at the time of the predator encounter (°A). The angle of deflection (°B) was then calculated in the direction of travel for the next hour. These angles were calculated by the following formula:

$$°A \; or \; °B = If\left(dX > 0, 90 - \left(\operatorname{atan}\left(\frac{dY}{dX}\right)\right) \times \left(\frac{180}{\pi}\right), 90 - \left(\operatorname{atan}\left(\frac{dY}{dX}\right)\right) \times \left(\frac{180}{\pi}\right) + 180\right)$$

$$If\ {}^\circ A\ or\ {}^\circ B > 180^\circ = {}^\circ A\ or\ {}^\circ B - 360$$

When possible, the speed of travel between each scan period was calculated by the following equation.

$$Speed = \frac{\left(\sqrt{dX^2 + dY^2}\right)}{\Delta Time}$$

2.6.2 Vegetation Density

An aerial photograph allowed us to extract all trees and shrubs in the field site. Using GIS, distances to the nearest tree or shrub were then calculated from all locations within the home range. Distances within zero to two meters were classified as high density (Figure 5), two to five meters were classified as medium density (Figure 6) and any distance greater than five meters was labelled as low density (Figure 7). These vegetation density classes were then overlaid on the home ranges of each troop.

Figure 5. An adult female and juvenile grooming in high density vegetation.

Figure 6. An adult male moving through medium density vegetation.

Figure 7. Vervets foraging in an area classified as having a low density of vegetation.

2.6.3 Before and after analysis

The change in behaviour of animal following a change in the environment can be assessed using a modified version of the Before- After-Control-Impact (BACI) assessment (Smith, Orvos & Cairns, 1993). This BACI method will examine the proportion of time spent vigilant before and after an encounter with a predator. Data collected prior to and following a vocal encounter with a non-lethal animal will be used as a control.

CHAPTER THREE

Results

3.1 Vegetation structure

The area has a relatively low species richness with 121 different plant species identified within the home ranges of the two study vervet troops. I identified three plant communities that could be grouped into two major structural units: open dwarf shrubland on the slightly higher lying and drier areas that continues into dense *Acacia karroo* woodland along the seasonal river (Figure 8).

Figure 8. Cross-sectional vegetation profile of the study area, indicating the three main communities. Courtesy of Leslie Brown.

The largest plant community (*Lycium oxycarpum* Dunal -*Acacia karro*o woodland) occurs along the river and floodplain and is dominated by the trees *Acacia karroo* and *Lycium oxycarpum* with the tree *Searsia lancea* Barclay and the tall shrub *Searsia longispina* Moffett prominent. Large single individuals (>6 m) of the pepper bark tree (*Schinus molle* L.) are scattered along the river bank. The woody species range in height from 1m to 5m and form dense canopies that cover up to 80% of the area. The herbaceous layer is dominated by the palatable grass *Panicum maximum* Jacq. and the pioneer grass *Cynodon incompletus* Nees. The two communities (*Pentzia globosa-Grewia robusta* Burret shrubland (to the west) and *Pentzia globosa-Cynodon incompletus* shrubland (to the east) extend on the higher-lying areas adjacent to the *Acacia* woodland and are both relatively open areas dominated by the dwarf shrub *Pentzia globosa* Less. and the tall shrub *Searsia longispina*. Whereas the woodland is still in very good condition, the shrubland communities are both degraded; a consequence of grazing in the former and cultivation in the latter prior to 1998.

3.2 Population Characteristics

3.2.1 Population Structure

I obtained repeated, reliable counts from 29 troops. This gave a mean troop size of 26.62 (+/-18.11 S.D.) for the population. Troops were, however, distinguished by whether their ranges were centered on the river or whether their source of water was artificial and maintained by humans. River troops (N=15) had a significantly larger mean size (40.13+/-15.53 S.D.) than troops relying on human-provided water (N=14. Mean=12.14 +/-3.23 S.D. $F_{1,27}=43.57$, $P<0.0001$. Figure 9). The sizes of the two study troops, occupying adjacent home ranges, were $N_{RBM}\approx 48$ and $N_{RST}\approx 72$ respectively. The modal adult sex ratio (M/F) was 0.67 for RBM ($N_{MALES}=10$, $N_{FEMALES}=15$) and 0.43 for RST ($N_{MALES}=10$, $N_{FEMALES}=23$).

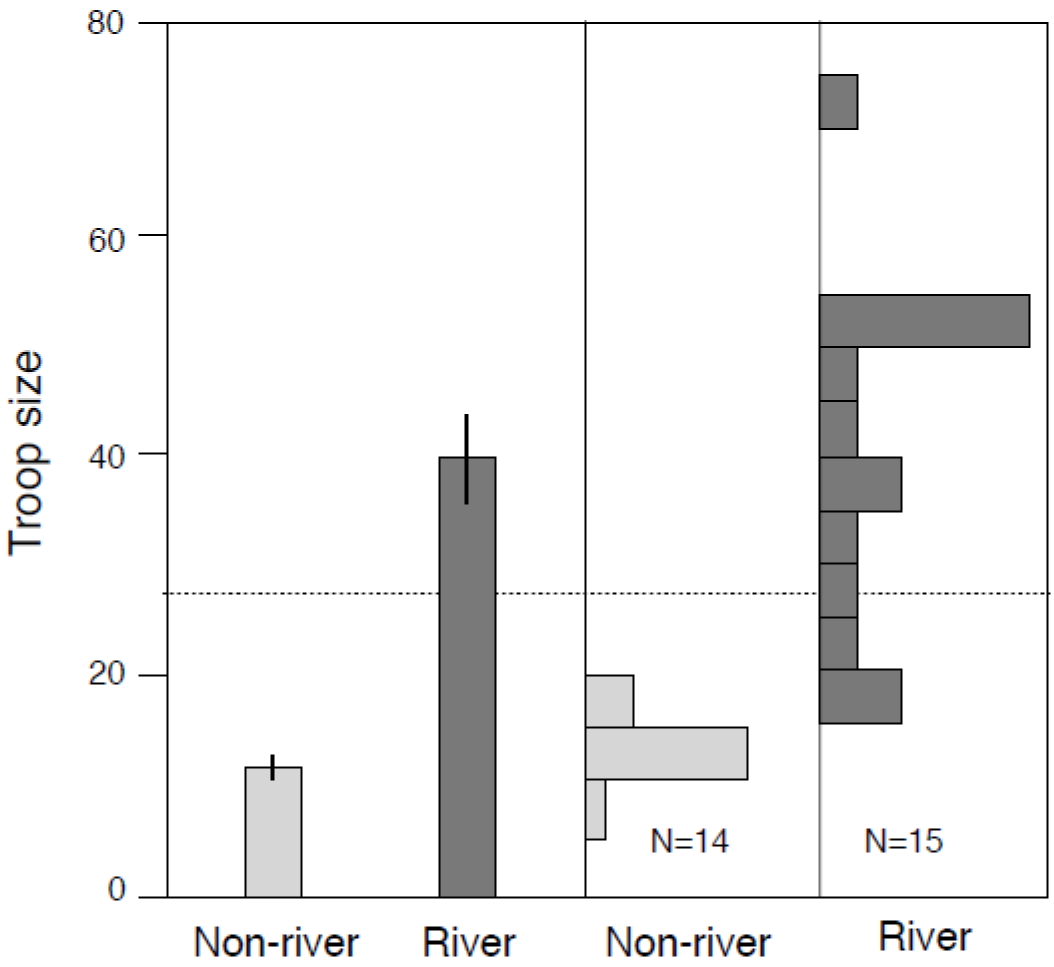


Figure 9. Mean troop size (+/- 1SD) and distribution for non-river and river-centred troops of the Samara game reserve, Mount Camdeboo and Asante Sana game reserve.

3.2.2 Inter-birth intervals (IBI)

I recorded 65 births over three years (N_{RBM}=30; N_{RST}=35), with a mean of 0.58 females giving birth each year ($Mean_{RBM}$=0.65; $Mean_{RST}$=0.53), allowing me to estimate an overall inter-birth interval of 20.6 months (RBM = 18.6 months; RST = 22.5 months).

3.2.3 Day Journey Length

I analysed 295 entire day journeys (N_{RBM}=138, N_{RST}=157). The mean distance travelled by RBM was 2806.3m (Range: 1013-5229m) while that for RST was 2353.6m (Range: 912-4320m). The data come from a year of low rainfall and both study troops frequently visited a distant water hole (N=100) during periods when there was no water available in their core areas (McDougall, et al., 2010). As this increased the mean day journey by more than 500m, I therefore ran a full-factorial ANOVA with Troop Identity, Season (Wet/Dry) and Water Hole Visits (Yes/No) as factors. The whole model was significant ($F_{7,287}$=11.22, Adj. R^2=0.195, $P<0.0001$) and there were significant main effects for Troop Identity ($F_{1,1}$=15.1, $P<0.0001$), Season ($F_{1,1}$=4.5, $P<0.05$. Mean $distance_{Dry}$=2760.3m, Mean $distance_{Wet}$=2387.8m) and for WaterHole Visits ($F_{1,1}$=32.75, $P<0.0001$. Mean $distance_{Yes}$=2972.3m, Mean $distance_{No}$=2431.97). The only significant interaction was for Season*Water Hole Visit ($F_{1,1}$=4.4, $P<0.5$), with visits to the water hole having a greater impact on day journeys in the wet season (Figure 10).

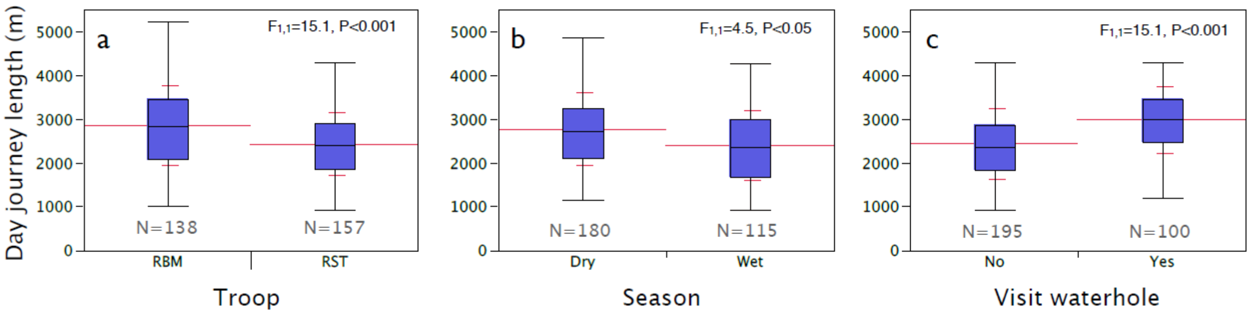


Figure 10. Box plots of the main effects of (a) Troop, (b) Season and (c) Waterhole visits on day journey length. Boxes indicate interquartile ranges and red lines indicate means and standard deviations.

3.2.4 Home range size and population density

I used the day journeys to estimate the annual home range sizes for the two study troops. RBM's 99% MCP covered an area of 176.1ha of which the four discrete core areas (50% MCP) constituted 10.45ha. They shared 23% of their home range with five other troops. RST used 63.7ha over the same period, with a single core area of 7.42ha. They shared 86% of their home range with 4 other troops (Figure 11). On the assumption that overlap areas were shared equally by the study troops and their neighbours (cf Whiten, et al., 1987), the data from RBM generate a population density of 30.79 animals/km^2, while the value for RST is 202.24 animals/km^2. Combining the data for RBM and RST and taking account of the 40.7ha overlap between their two home ranges, provides a composite population density estimate of 54.68 animals/km^2. I estimated the defendability of these home ranges (A) in relation to the average day journey length, using Mitani and Rodman's (1979) defendability index (D), where D=d/d' and d' =

(4A/∏). Where $D \geq 1$, home ranges are assumed to be defendable. The values for Samara were computed as $D_{RBM}=1.24$; $D_{RST}=2.83$.

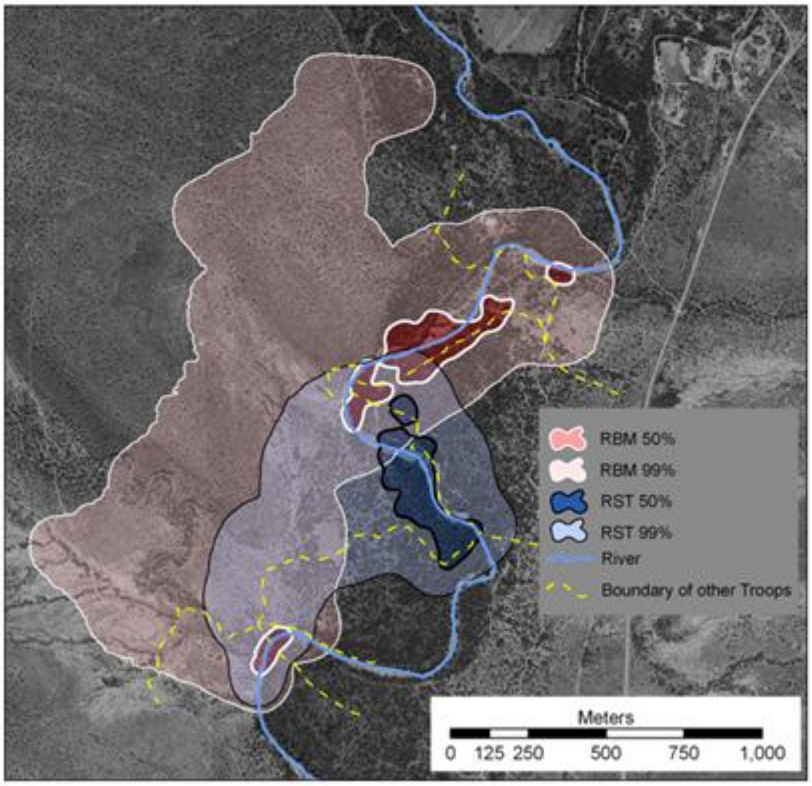
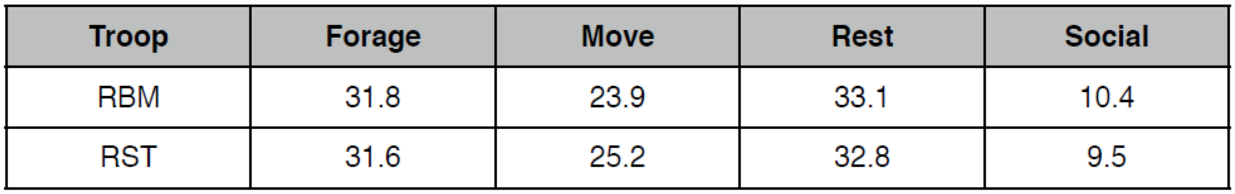


Figure 11. Home ranges of the study troops, indicating core areas and overlap.

3.2.5 Activity

The relative allocation of time by the two troops to the four activity categories is provided in Table 4.

Table 4. The annual percentage of adult scan samples allocated to each of four activities.



Troop	Forage	Move	Rest	Social
RBM	31.8	23.9	33.1	10.4
RST	31.6	25.2	32.8	9.5

3.3 Diet

The animals foraged on 27 different plant species as well as a fungi species and a number of different insects, of which grasshoppers and termites were eaten most frequently (Table 5). The five most frequent items in the diet accounted for 68.7% of annual foraging effort. *Acacia karoo* products alone accounted for 33.8% of all foraging records and were used consistently across the 10 months (Figure 12).

Table 5. Food species and plant parts consumed by vervet monkeys at Samara Game Reserve.

Food species	Parts consumed	number of scans	Percent intake
Acacia karoo	Gum, seeds, flowers, leaves	3159	33.80
Atriplex semibaccata R.Br.	Berries	1543	15.33
Insects	-	778	7.73
Lycium oxycarpum	Berries, leaves	651	6.47

Schinus molle	Berries	548	5.44
Lycium cinereum Thunb.	Berries, leaves, flowers	475	4.72
Asparagus retrofractus L.	Leaves, roots	453	4.6
Mesembryanthemaceae family	Leaves	452	4.49
Helictotrichon turgidulum (Stapf) Schweick	Leaves	304	3.02
Grewia robusta A. Cunn.	Berries, flowers	243	2.41
Carissa bispinosa (L.) Desf. ex Brenan.	Berries	194	1.93
Sceletium sp.	Leaves	168	1.67
Rhus lancea	Berries	150	1.49
Rhus longispina	Flowers	145	1.44
Unidentified items on ground	-	133	1.32
Sansevieria sp.	Leaves	86	0.85
Grasses (Cynodon incompletus; Panicum maximum)	Leaves	84	0.83
Chenopodium sp.	Leaves	74	0.74
Mesembryanthemaceae family	Leaves	64	0.64
Diospyros lycioides De Winter	Berries, flowers, leaves	46	0.46

Pentzia globosa Less.	leaves	21	0.21
Boscia albitrunca Gilg. & Ben.	Berries	20	0.20
Funghi	Mushroom	8	0.08
Portulacaria afra Jacq.	Leaves	5	0.05
Cactus sp.	Leaves	5	0.05
Gymnosporia buxifolia Szyszyl.	Berries	1	0.01
Euclea crispa Thunb.	Leaves	1	0.01
Aloe ferox Mill.	Flowers	1	0.01

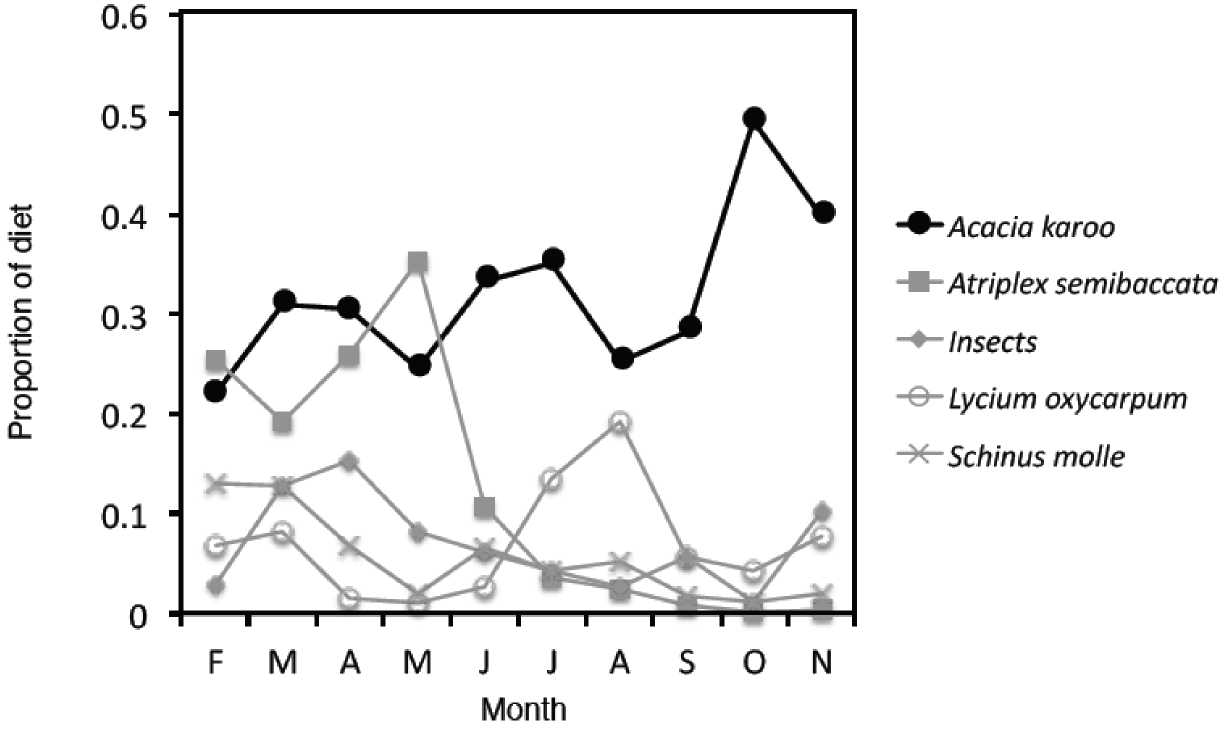


Figure 12. Contributions of the five most commonly used food sources to monthly foraging effort.

3.3 Body mass

Adult males weighed 5.93kg (+/-0.42 S.D. N=9) and females weighed 3.3kg. (+/-0.3 S.D. N=13). These are compared to values from other populations in Figure 13.

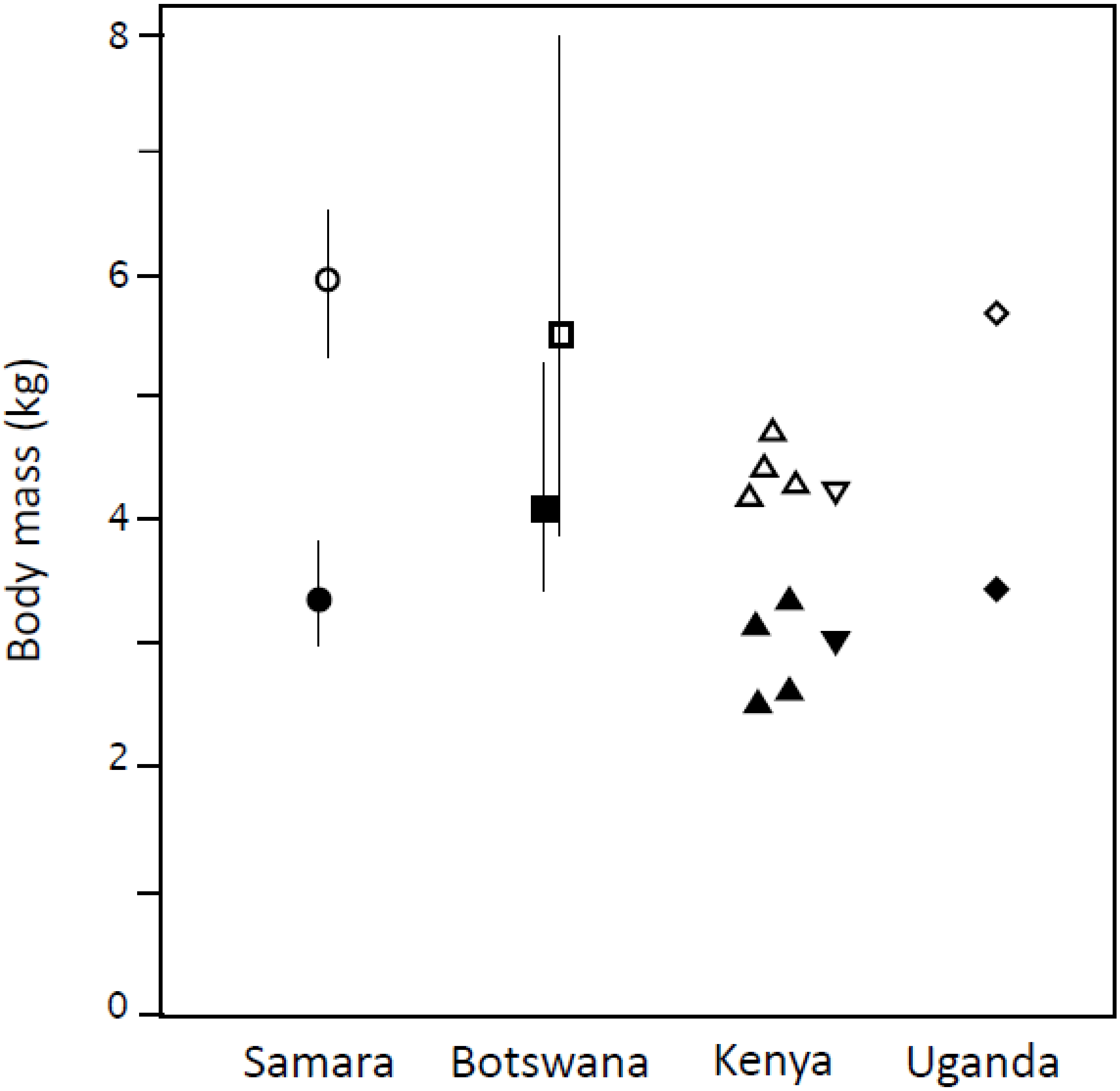


Figure 13. Comparison of body mass across different vervet monkey populations. Where available, standard deviations are indicated. Each symbol identifies a particular population. Open symbols: adult males; solid symbols: adult females. Data for Botswana (squares) from Skinner and Chimimba (2005); Kenya (triangles) from Kagira et al. (2007) and Turner et al (1997); Uganda (diamonds) from Bolter and Zihlman (2003).

3.4 Vegetation Density

A spatial map was constructed to illustrate the three vegetation density classes that make up both RST and RBM's home ranges (Figure 14). RST's home range is made up of 62% high density, 23% medium density and 15 % low density vegetation. This is in comparison to RBM's home range which is made up of 33% high density, 34 % medium density and 33% low density vegetation. If corrected for the proportion of vegetation density that is found in the respective troops home ranges, RBM spends significantly more time than expected in high density vegetation (x^2= 19.8, d.f = 2, $P < 0.001$) and significantly less time than expected in low density vegetation (x^2=10.0, d.f=2, $P < 0.001$).

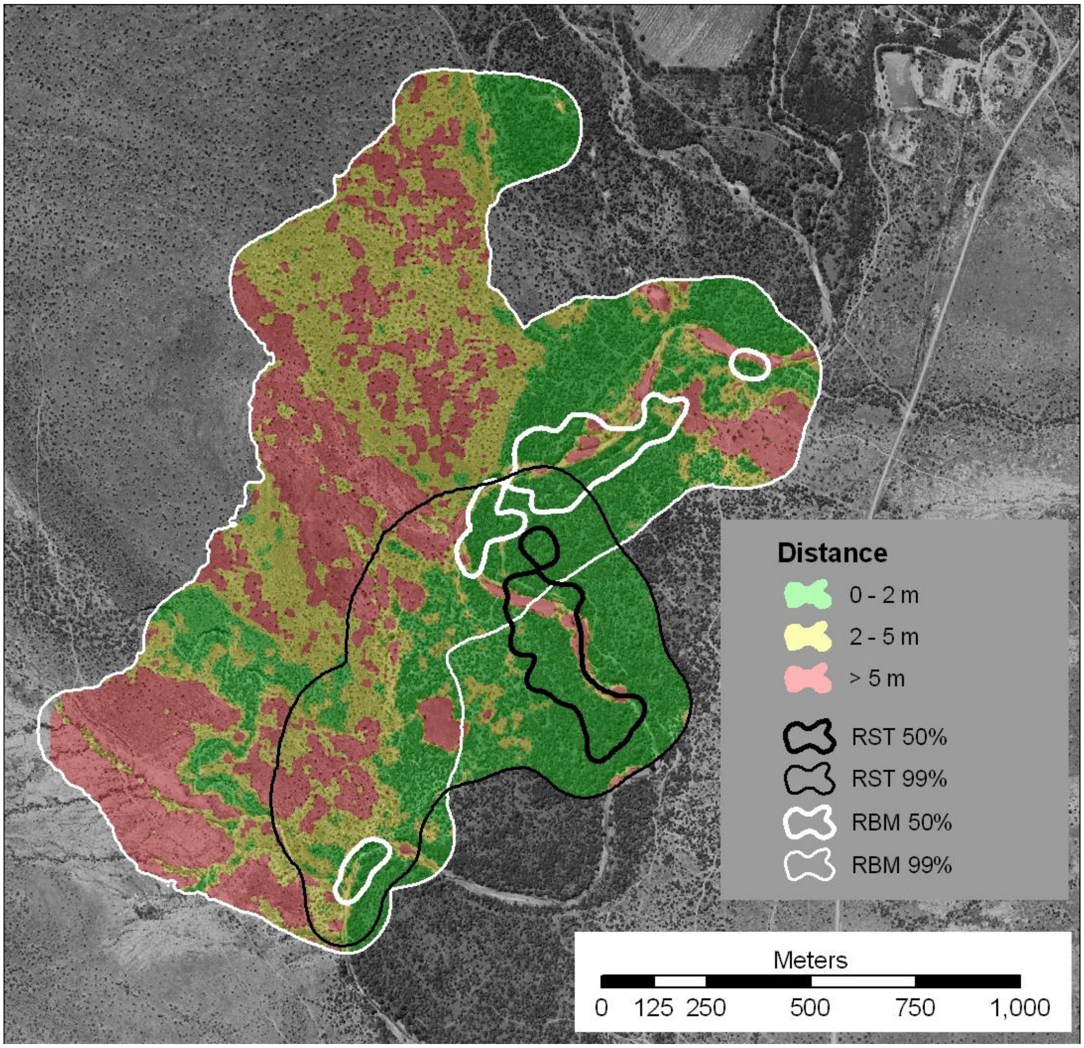


Figure 14. Vegetation density classes overlaid on the home ranges of RST and RBM. The thin black and white polygons refer to the area where RST and RBM spend 99 % of their time respectively. The thick black and white polygons refer to the area where RST and RBM are found 50% of the time, respectively. The 0-2 m, 2-5 m, and > 5 m classifications refer to high, medium and low vegetation density areas, respectively.

3.5 History of Predator Encounters

Given that female vervet monkeys are philopatric and males do not leave the troop until reaching adulthood, it is reasonable to assume that a sudden disappearance, of previously healthy, female or juvenile vervet is a result of a predator attack. The 2009 season saw one caracal attack where the female was injured but did not die. Additionally, partial remains of two juvenile monkeys were found in the field site throughout 2009. During 2010, four adult females died, two of which are assumed to have been killed from snake bites. Eight infants died of unknown causes. Another female was attack by a caracal but escaped with a broken jaw and minor cuts to her face. In the season following, January 2011-Oct 2011, there were three adult females, one juvenile and three infant monkeys that went missing. Two of these bodies were found and necropsies performed by a veterinarian found that puff adder venom was the cause of death. Although snakes in the area do not actively prey on vervets, the results of the necropsies provide evidence that snakes are indeed a source of extrinsic mortality, as is the case in other field sites (Cheney & Seyfarth, 1980; Strusaker, 1967a).

3.6 Frequency of predator encounters (2011)

There were 154 predator events recorded for RST and 146 recorded for RBM. RST had more overall avian and snake encounters than RBM but had less encounters with other predator specific guilds (Figure 15). However, when the total number of predator encounters are corrected for the number of observational days spent on each troop, neither troop encountered significantly more predators (x^2=0.110, df=1, $P > 0.05$).

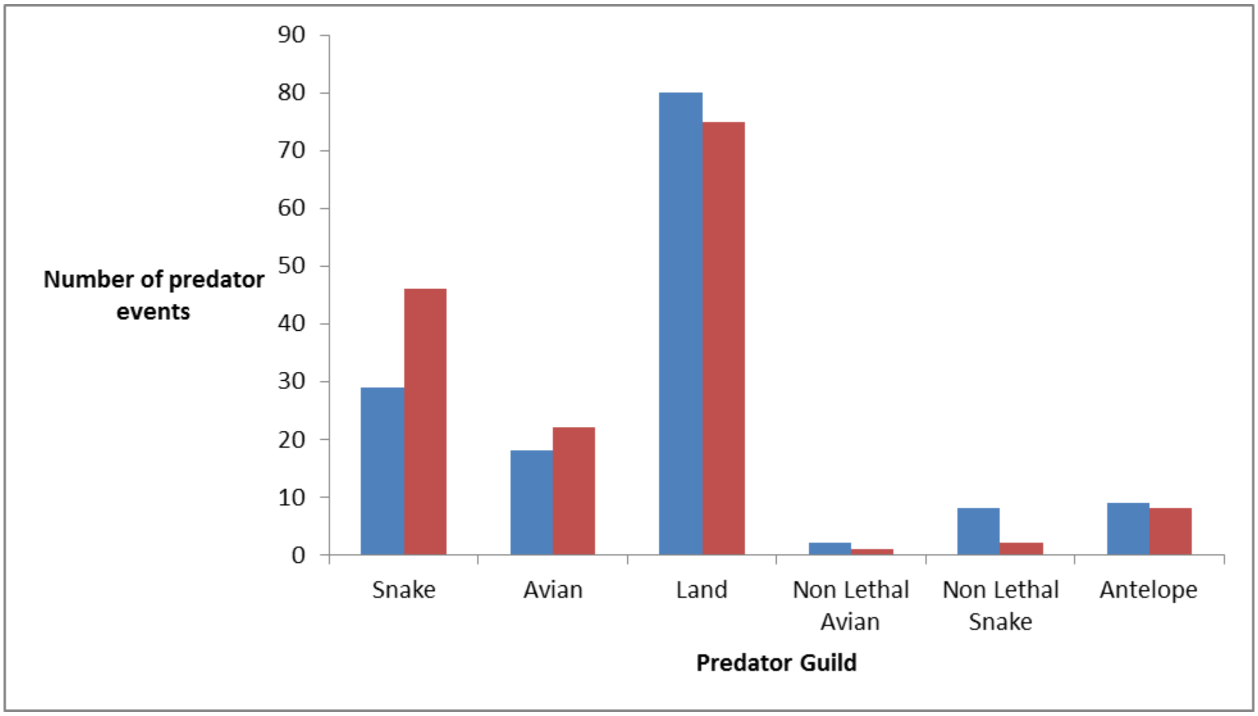


Figure 15. The number of predator guild specific encounters with respect to each troop. RBM is indicted by blue and RST is indicated by red (N=300).

3.7 Location and reaction time to predator encounters

Predators were not encountered significantly more in any of the vegetation classes (Table 6). The reaction times, measured by duration of calls, between RBM and RST to a land predator encounter were not significantly different (Kolmogorov–Smirnov, d_{max}=0.106, n1=75, n2=80, x^2=1.4, P=0.4). Together the reaction times, to encounters with avian, land, snake and non-lethal predators are shown in Figure 16. The reaction time increases significantly following an encounter with a land predator when compared to a combination of avian and snake predator guilds (Kolmogorov-Smirnov, d_{max}=0.52, n1=155, n2=115, P<0.001).

Table 6. Chi-squared statistic for comparisons between different vegetation classes and number of predator sightings.

Vegetation Class	1	2	3
X^2	0.166	0.104	0.291
df	2	2	2
P	>0.05	>0.05	>0.05

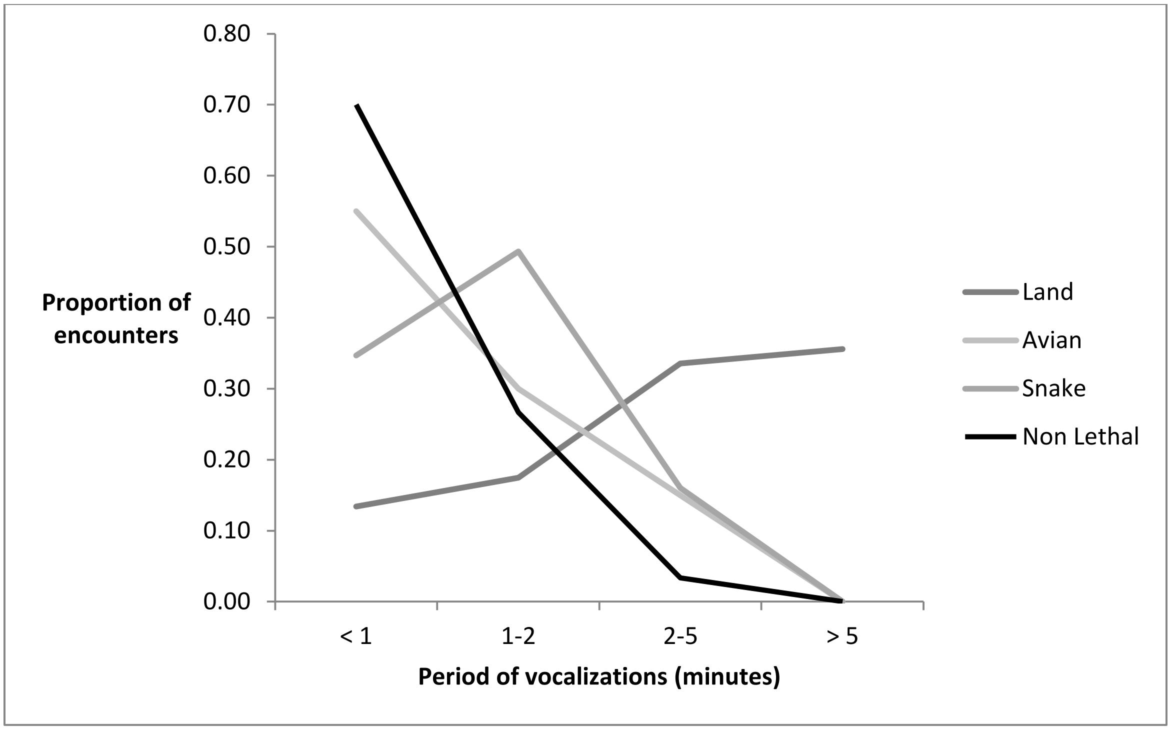


Figure 16. RBM and RST combined reaction time following an encounter with four predator classes. Land predators are represented with dark grey, avian with lightest grey, snake with medium grey and the non-lethal encounters with black.

3.8 Vigilance without predators

The objective of the following analysis was to determine whether the factors of sex, troop identity, vegetation density or location within the environment had an effect on the proportion of time spent predator vigilant. Given the binary nature of predator vigilance, I performed a mixed logistical regression because an examination of the data, through both model comparison and an examination of variance components, revealed that the identity of the monkey and data collector to be salient sources of variance. I considered the effects of the following four covariates:

1) Sex: Female or Male
2) Troop Identity: RBM or RST
3) Vegetation Density: High, Medium and Low
4) Location: Ground, Open, Tree, Shrub

Given the relatively small number of covariates, I considered all possible models and the empty model as a baseline for comparison. Model comparison revealed the model with all covariates to be the best-fit, within the context of the candidate set. This model (log $\mathcal{L}$ = -7779.35, k = 10, AIC = 15578.7), carried essentially all of the available model weight (i.e. $w_i \approx 1$) and, as such, I can be certain that it provides the best characterisation of the data, given the variables available. The results of the analysis mentioned above can be found in Table 7.

Table 7. Determinants of change in the proportion of time spent vigilant. The intercept describes the probability of vigilance performed by a female on the ground in high density vegetation (N=42,619).

Fixed effects	Estimate Std.	Error	z Value	Pr (> abs(z))
Intercept	-3.78462	0.64258	-5.890	3.87E-09
Sex	-0.90614	0.10064	-9.004	< 2E-16
Open	0.79053	0.06696	11.806	< 2E-16
Shrub	0.29570	0.07168	4.125	3.7E-05
Tree	0.75883	0.05571	13.603	< 2E-16
Medium Density	0.95017	0.05341	17.791	< 2E-16
Low Density	1.26533	0.06206	20.388	< 2E-16
RST	-0.48782	0.09282	-5.255	1.48E-07

The intercept describes the probability of vigilance performed by a female on the ground in high density vegetation. To interpret the data as probabilities however, I transformed the linear equation of the model using the inverse-logit transformation equation

$$\frac{\exp(x)}{1+\exp(x)}$$

At first glance, the model appears to predict that sex has a strong effect on vigilance. However, Figure 17 shows that the observed difference between the sexes was minimal and once the model is transformed it predicts only a weak effect, which confirms what was observed.

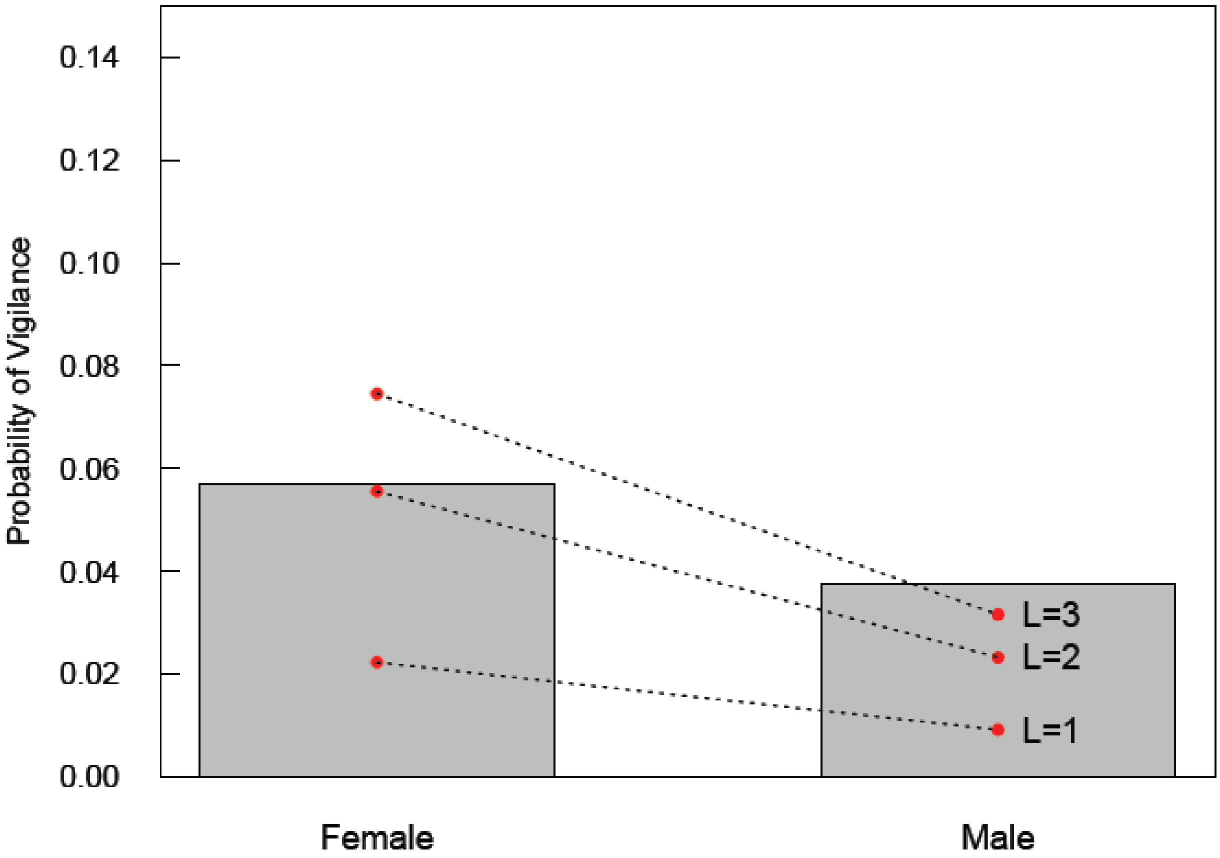


Figure 17. Relationship between sex and the probability of predator vigilance. The bars indicate the observed probability of predator vigilance by males and females. The lines describe the effect of sex predicted by the model. The different lines indicate this effect in different vegetation densities with 1, 2, and 3 representing high, medium and low density vegetation.

Similarly, when the effect of troop identity is measured, it too has relatively little effect (Figure 18). Specifically, it shows that the probability of observing vigilance in RST was only marginally smaller than in RBM. The model predicts this minimal effect well (Figure 18).

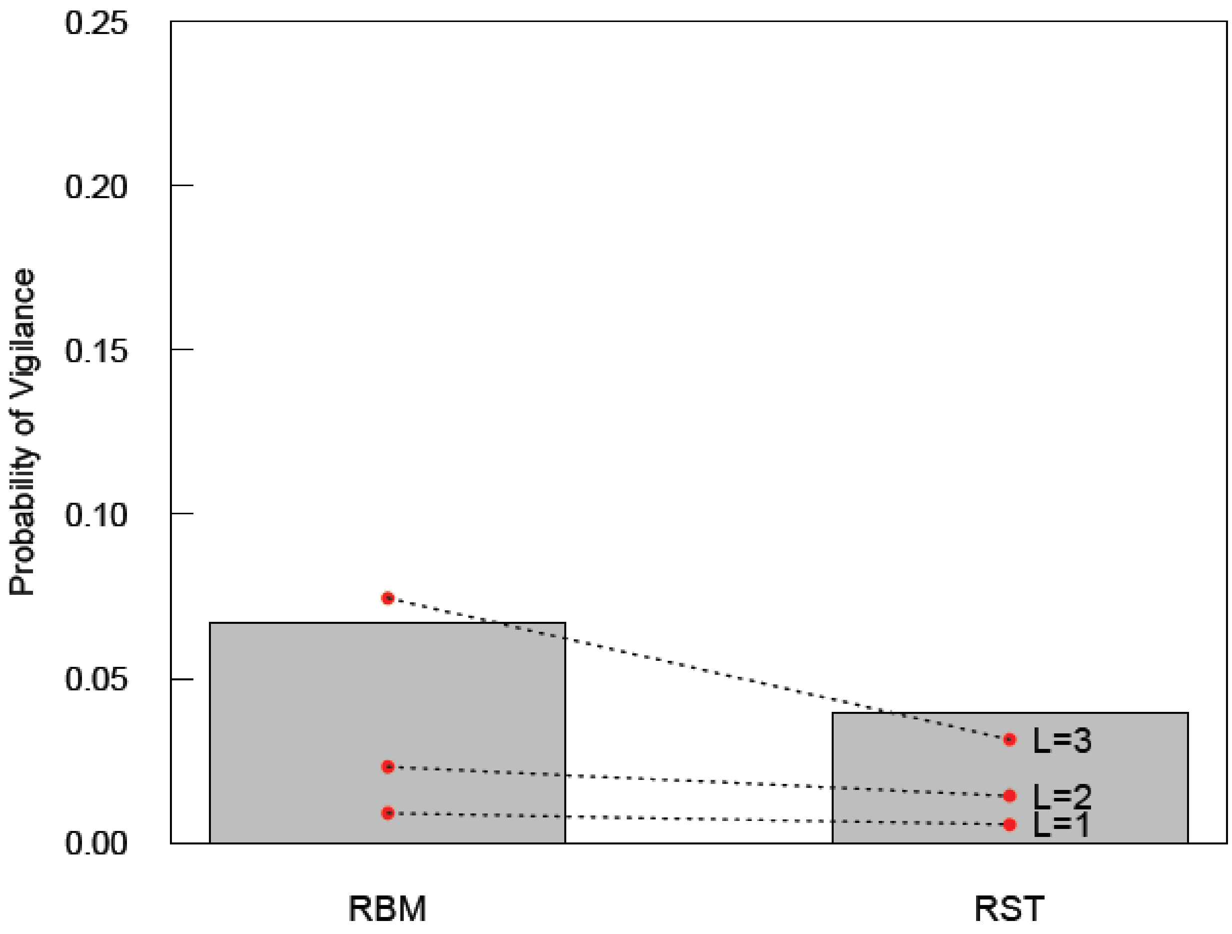


Figure 18. Relationship between troop identity and the probability of vigilance. The bars indicate the observed probability of vigilance in each troop. The dotted lines describe the effect of troop predicted by the model. The different lines indicate this effect in different vegetation densities with 1, 2, and 3 representing high, medium and low density vegetation.

With respect to the location of the individual (Ground, Open, Tree, Shrub), there were no dramatic effects but an obvious pattern emerged (Figure 19). It appears that individuals tend to be more vigilant when in open country; that is, the probability of observing vigilance was higher when sampling individuals that were defined as being in the open.

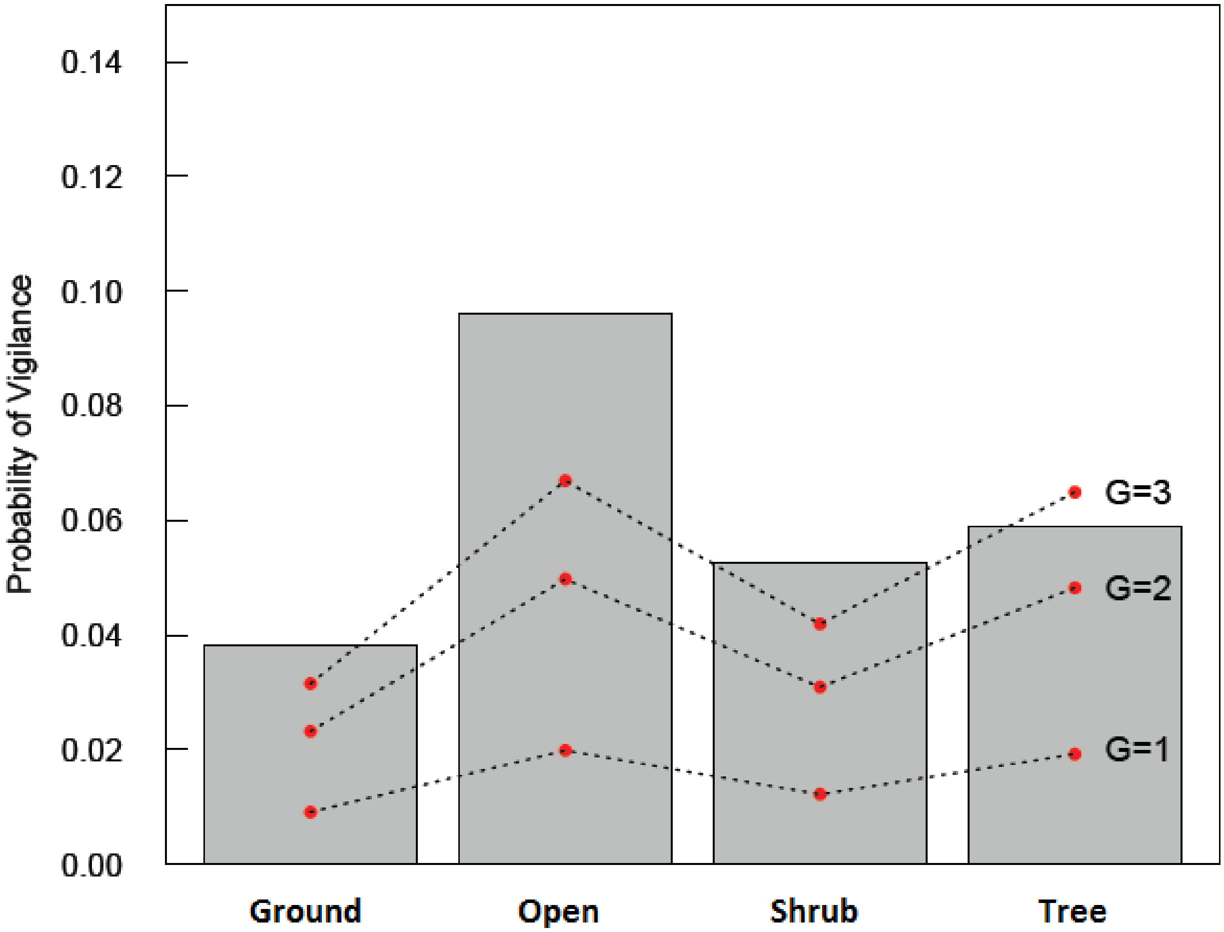


Figure 19. The relationship between location and the probability of vigilance. The bars indicate the observed probability of vigilance in each location. The lines describe the effect of location predicted by the model. The different lines indicate this effect in

different vegetation densities where 1 represents high density vegetation, 2 represents medium density vegetation and 3 represents low density vegetation.

In addition, there is some suggestion that individuals may be more vigilant when in trees and shrubs; although, this effect is much weaker. The model predicts all these effects well. Lastly, the effects of vegetation density are shown in Figure 20. There is a positive increase in the probability of observing vigilance as the density of vegetation decreases.

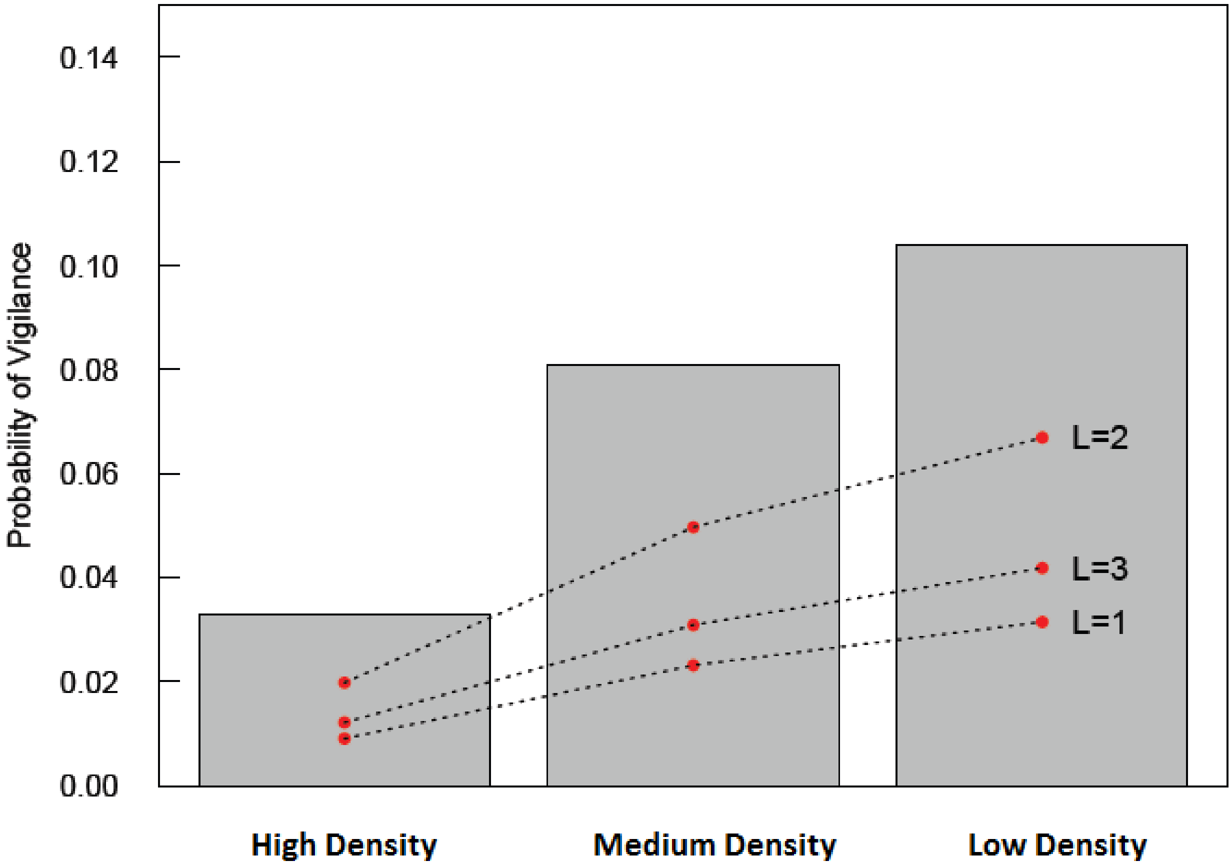


Figure 20. The relationship between vegetation density and the probability of vigilance. The bars indicate the observed probability of vigilance in each vegetation density class. The lines describe the effect of vegetation density predicted by the model. The different lines indicate this effect on the ground represented by the number 1, in the open represented by 2 and in a tree or shrub represented by 3).

3.9 The effect of an alarm-call inducing encounter with other species on patterns of vigilance

I had two objectives in this analysis. The first was to assess the effects of different call-eliciting species on subsequent vigilant rates and the second was to determine whether the interaction between vigilance types and different call-eliciting species might allow the ‘unidentified’ vigilance category to be re-assigned to one of the other two categories.

To determine the consequences of encounters with other animals that resulted in the production of alarm calls by one or more troop members, I compared the relative proportion of vigilance records allocated to different vigilance types, in the context of the animal eliciting the calls, in the 60 minute before a predator-alarm call with that in the 60 minutes following the call. The analysis was restricted to this time band as Figure 21 indicates that shifts in the hourly proportions of social and predator vigilance were most marked then. I ran the arcsin-transformed proportions of vigilance records in a MANOVA with proportions before and after alarm-calling as repeated measures (‘TIME’). I entered VIGILANCE (Predator, Social, Unknown and Not Vigilant) and ELICITOR (Antelope, Land Predators (Jackal, caracal, cheetah), Birds, Snakes and Snake/Bird) and factors in a full-factorial model. I restricted the analysis to these variables as I wanted to be able to detect broad shifts only and visual inspection of graphs indicated that neither the sex of the subject nor troop membership were likely to have an effect. The results of the tests of with-in subject effects are provided in Table 8 and indicate that neither TIME nor the TIME*ELICITOR interaction were significant. The TIME*VIGILANCE interaction was significant and visual inspection of the marginal means indicates that, as suggested in Figure 22, this was due to a direct trade-off between the upward shift in predator-vigilance and a downward shift in the absence of recorded vigilance across the two time periods (Figure 21). The three-way interaction - TIME*VIGILANCE*ELICITOR - was also significant and the transform parameter estimates suggest that this was due to an increase in predator-vigilance in the hour following encounters with Land Predators. The data suggest that 'unknown' vigilance may be closer to the pattern of social vigilance (Figure 22).

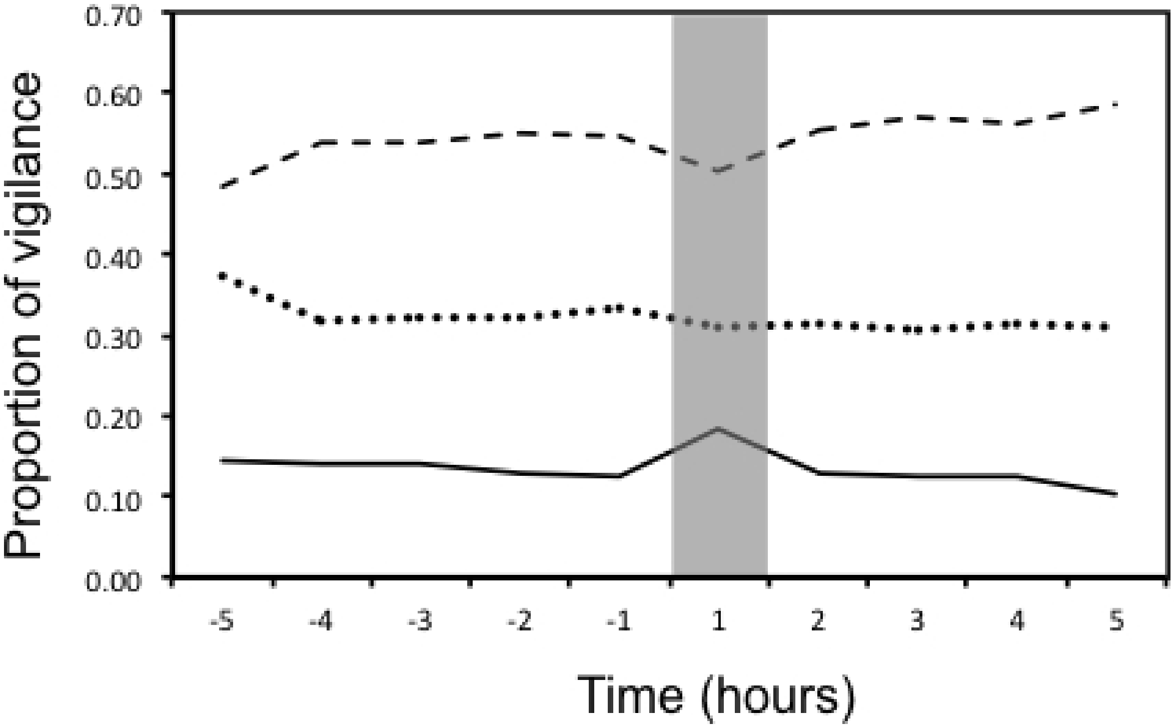


Figure 21. Proportion of time spent vigilant before (-5 to -1 hours) and after (1 to 5 hours) a predator encounter. The dashed line, dotted line and solid line represent the proportion of time spent social vigilant, unknown vigilant and predator vigilant, respectively. (N = 11,113 scans). The grey bar highlights the hour following a predator encounter.

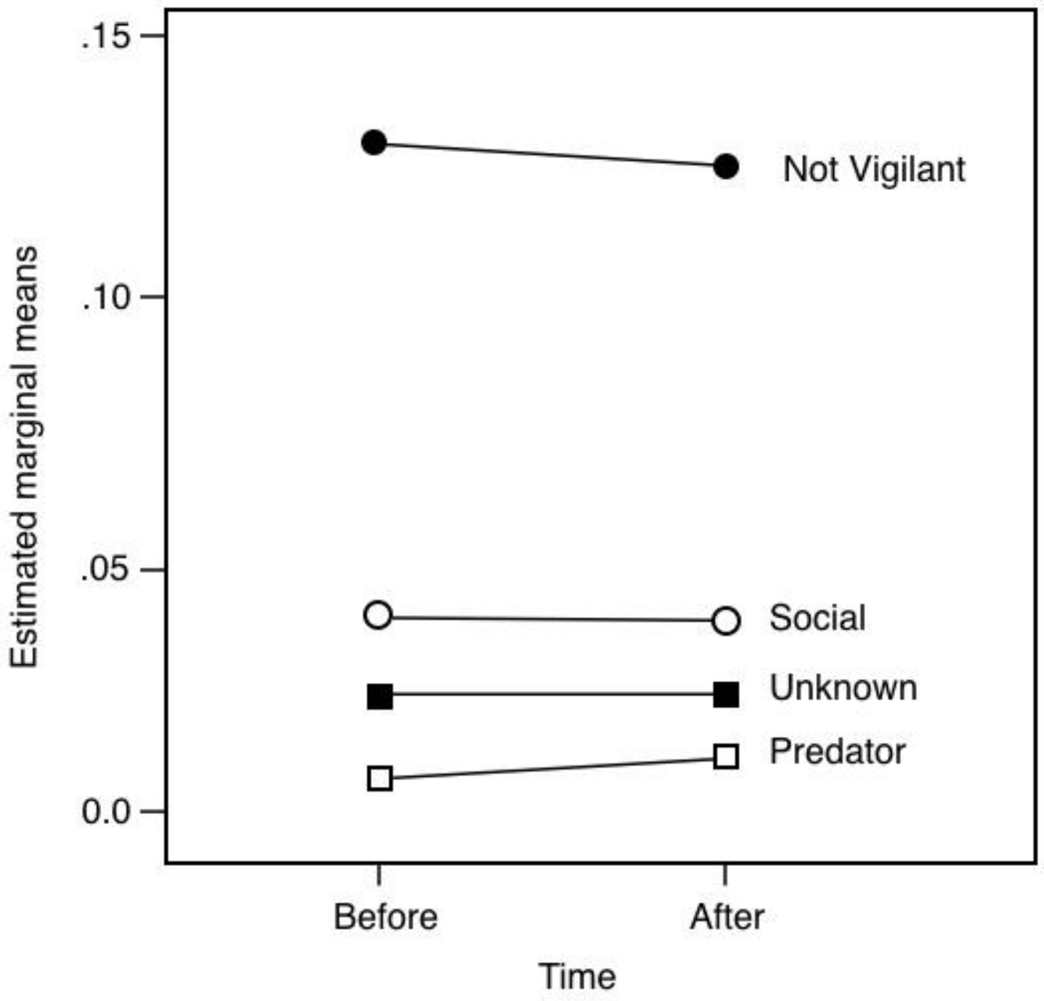


Figure 22. Estimated marginal means for the different vigilance types an hour before and an after an encounter with a land predator.

Table 8. Tests of with-in subject effects on the proportional representation of different vigilance types before and after alarm-calling. (N=11,160).

Source	DF	SS	MS	F	P
TIME	1	3.77E-06	3.77E-06	0.007	0.93
TIME*VIGILANCE	3	0.006	0.002	3.58	0.013*
TIME*‘ELICITOR’	4	0.003	0.001	1.42	0.223
TIME*VIGILANCE*ELICITOR	12	0.026	0.002	4.2	0.0001*
ERROR (TIME)	1140	0.59	0.001		

3.9 Responses to potential predators

In order to determine the effect of encountering a potential predator on habitat occupancy, I used the approach of Henzi et al (1998) to compare the direction of travel after a predator encounter in relation to the estimated direction of travel, had the encounter not occurred. Following the finding (above) that predator vigilance increased in response to encounters with land predators, I tested the following two predictions:

i. That encounters with land predators would be followed by a greater angle of deviation (i.e. travel away from the encounter site than would encounters with other potential predators (large birds, snakes). This prediction is also driven by the expectation that sustained movement away from the point of contact would not reduce the likelihood of predation by avian predators, nor the likelihood of attack by snakes.

ii. That there would be a positive correlation between the angle of deviation and the speed of movement away from the encounter location.

I entered the absolute angle of deviation as the dependent variable in a full factorial model, with habitat type (VEG_INDEX - scored as 1-3) and predator type (PREDATOR) as factors and speed (SPEED) as a covariate. The results indicate that no independent variable, either as a main effect or in interaction with others, was able to explain the change in angle following an encounter with a predator (Whole model: $F_{11,154}$=1.07, P=0.38; Adj. R^2=0.005. Table 9).

Table 9. Determinants of change in absolute angle of travel following an encounter with a predator.

Source	DF	SS	F	P
SPEED	1	3655.46	1.19	0.27
VEG_INDEX	2	205.2	0.03	0.96
SPEED*VEG_INDEX	2	212.38	0.03	0.96
PREDATOR	1	965.29	0.31	0.57
SPEED*PREDATOR	1	930.64	0.3	0.58
VEG_INDEX*PREDATOR	2	3519.0600	0.57	0.56
SPEED*VEG_INDEX*PREDATOR	2	3468.57	0.56	0.56

CHAPTER FOUR

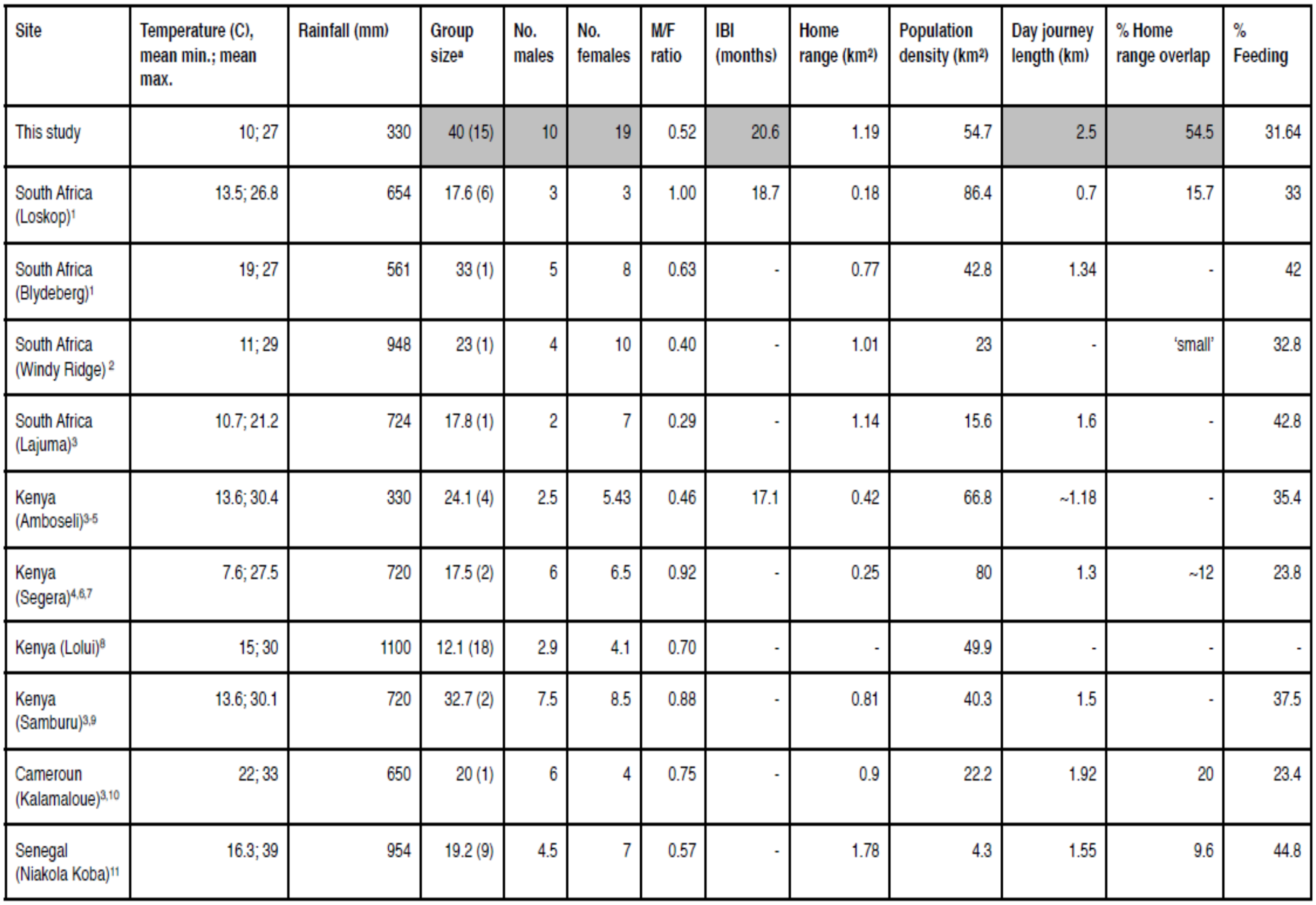
Discussion

The data indicate a significantly larger mean troop size for those karoo vervet troops whose ranges center on local rivers. Colonization of areas away from these rivers is made possible by the presence of artificial water points but carries the corollary that the animals are confronted by habitat that is naturally less productive, currently degraded and may increase the risk of predation due to lack of adequate sleeping sites. This would explain their small troop size and suggests a vulnerability to downturns in local environmental conditions. Indeed, at least three non-river troops that were monitored in 2009 as part of the census were no longer locatable by the end of 2010, over which period the local drought had worsened. While the presence of water means that their disappearance was likely to have been associated with a decline in food availability, it is not known whether they suffered extirpation or had returned to the river and fused with troops there (Isbell, et al., 1991).

The absence of artificial water points along the Melk River and the relative lack of degradation of the riparian habitat suggest that river-centered troops constitute the ‘natural’ regional population and can therefore be used to characterize the response of the species to these narrow habitable corridors that run through an otherwise inhospitable landscape. Perhaps the most surprising finding in this regard, given the inability of the activity budget models to predict their presence in the region, is that they are not a marginal population but an apparently flourishing one, with most parameter values used to determine population viability well within the range of those reported from other study sites (Table 10; Figure 6).

Table 10. Comparative data for different vervet monkey populations arranged by latitude. IBI=Inter-birth intervals. Grey fill indicates values for the study population that are distinctive.Primary data from: 1. Barrett (2004, 2009, pers. comm.), 2. Baldellou (1992, pers. comm.), 3. Willems (2007). 4.Enstam and Isbell (2007), 5. Struhsaker (1967) 6. Isbell (pers. comm.), 7. Pruetz (2009) 8. Hall and Gartlan (1965), 9. Whitten (1983), 10. Nakagawa (1999), 11. Harrison (1983, 1985).

a. Numbers in parentheses indicate number of groups used to derive group sizes.



Site	Temperature (C), mean min.; mean max.	Rainfall (mm)	Group size[a]	No. males	No. females	M/F ratio	IBI (months)	Home range (km^2)	Population density (km^2)	Day journey length (km)	% Home range overlap	% Feeding
This study	10; 27	330	40 (15)	10	19	0.52	20.6	1.19	54.7	2.5	54.5	31.64
South Africa (Loskop)[1]	13.5; 26.8	654	17.6 (6)	3	3	1.00	18.7	0.18	86.4	0.7	15.7	33
South Africa (Blydeberg)[1]	19; 27	561	33 (1)	5	8	0.63	-	0.77	42.8	1.34	-	42
South Africa (Windy Ridge)[2]	11; 29	948	23 (1)	4	10	0.40	-	1.01	23	-	'small'	32.8
South Africa (Lajuma)[3]	10.7; 21.2	724	17.8 (1)	2	7	0.29	-	1.14	15.6	1.6	-	42.8
Kenya (Amboseli)[3-5]	13.6; 30.4	330	24.1 (4)	2.5	5.43	0.46	17.1	0.42	66.8	~1.18	-	35.4
Kenya (Segera)[4,6,7]	7.6; 27.5	720	17.5 (2)	6	6.5	0.92	-	0.25	80	1.3	~12	23.8
Kenya (Lolui)[8]	15; 30	1100	12.1 (18)	2.9	4.1	0.70	-	-	49.9	-	-	-
Kenya (Samburu)[3,9]	13.6; 30.1	720	32.7 (2)	7.5	8.5	0.88	-	0.81	40.3	1.5	-	37.5
Cameroun (Kalamaloue)[3,10]	22; 33	650	20 (1)	6	4	0.75	-	0.9	22.2	1.92	20	23.4
Senegal (Niakola Koba)[11]	16.3; 39	954	19.2 (9)	4.5	7	0.57	-	1.78	4.3	1.55	9.6	44.8

There are two values, however, that might be assumed to indicate ecological stress. The first is the slightly longer interbirth intervals in relation to those reported from the long-term study at Amboseli and the second is the longer day journey lengths that characterize my two study groups. Both are explicable in terms of increased group size, with intragroup competition leading to lower reproductive rates and larger groups needing to cover more ground in order to forage (Clutton-Brock and Harvey 1977, Borries et al. 2008). The latter is corroborated by data from 12 troops (Barrett, 2009; Willems, 2009; this study) that indicate a positive correlation between troop size and day journey length (r_s=0.78, N=12, P<0.001).

What therefore requires explanation are the distinctively large size of river-centered groups and - given that vervet monkeys are a territorial species (Struhsaker, 1967) - the marked extent of home range overlap. In the absence of indications of gross ecological stress, the large troops living at high densities are clearly being sustained by the consistent availability of *Acacia karroo* products, as was much the same for the historically high density population of vervets at Amboseli in Kenya, where *A. xanthophloea* Benth. and *A. tortilis* Hayne played much the same role (Struhsaker, 1967; Lee & Hauser, 1998). At the same time, the inclusion of both insects and succulents in the diet (Pasternak et al. in prep.), buffered the animals during those periods when free-standing water was absent (McDougall et al., 2010). While one might expect some broad positive relationship between group size and population density (van Schaik, 1983), three things suggest that this will not provide an adequate explanation for population structure at Samara. The first is that there is no indication of a correlation between density and troop size for the vervet populations in Table 10 (r_s=-0.09, N=11, P=0.77). The second is that mean troop size was very much smaller at a number of other sites where density was comparably high (Table 10). The third is that the time budget model for vervet troop size derived by Willems and Hill (2009a) predicts a maximum ecologically tolerable troop size of 46 animals at Samara (Henzi et al. in prep., using adult female activity budget values). Whereas the maximum troop size exceeded observed sizes for almost all their populations (Fig. 6 in Willem and Hill 2009), both my study troops exceeded model predictions. One possibility, of course, is that predation risk is responsible (van Schaik, 1983).

Predation rates are extremely difficult to calculate in primates due to the degree of difficulty in observing a predator attack. The disappearance of troop members, particularly adult males, is subject to various possible explanations and actual reports of predator attacks seem to be based on circumstantial evidence. This makes it difficult to determine the predator guilds that are responsible for the majority of deaths. Comparing predation rates across field sites is increasingly problematic. For example, the hours of observation and the number of observers utilized in each field site will inevitably impact the observed frequency of predator attacks. Regardless, it is important to note that our two troops have not experienced the local extirpations that have occurred within other vervet field sites that are thought to be a result of high kill rates (Isbell, 1990). Most likely, this is a result of missing predator species such as leopards, constricting snakes and predatory baboons. This lack of predator diversity theoretically reduces the risk of night attacks and increases the safety of vertical substrate use such as trees. Although calculating and comparing predation rates is difficult, the perceived risk of predation, measured through the use of predator vigilance and its impact on space use will help identify the influence predators have on this population and will allow for comparison with other populations.

Studies examining predation typically use some form of vigilance to determine risk. However, Treves (2000) highlighted numerous studies which saw a single definition of vigilance, and highlighted a need for a quantitatively tested definition separating social and predator vigilance.

The results shown in Figure 21 indicate that social and predator definitions of vigilance respond to predator encounters differently and predator vigilance increases following an encounter with a land predator only. There is trade-off between predator vigilance and the absence of recorded vigilance following an encounter, whereas as social and unknown vigilance is unaffected. This result suggests that it is possible to discriminate between predator and social vigilance. Additionally, it shows that vervets are trading off the costs of being vigilant with the benefit of keeping track of a land predator's location for a period of time following an encounter. This, along with the result that vervets spend on average more time calling at land predators, suggests that land predators are viewed as the greatest source of risk to these vervet.

Before a comparison on vigilance can be made between other field sites the differences between the study troops must first be established. The vegetation density of an environmental is known to influence the perceived risk of predation in vervets. The varying proportions of vegetation classes that comprise both RBM and RST's home range highlight some of the differences in landscape that each troop utilizes on a daily basis and may result in each troop and may influence the level of predation risk. However, the different make-up of the environment, along with the observation that

RBM does spend significantly more time than expected high density vegetation does not appear to influence the rate at which they encounter predators. Furthermore, neither troop reacts differently to each predator in terms of reaction time nor is there a significant difference in the proportion of time spent predator vigilant. This absence of a group size effect in vigilance requires a further explanation. Isbell and Young (1993b) found a negative correlation between the proportion of time spent vigilant and the troop size in vervets. This study, as previously mentioned, failed to remove the effects of sex and dominance. The statistical model used in this study examines each effect separately and separates social vigilance from within group vigilance as recommended by Treves (2000). The lack of a group effect found in this study and in other primates (Cowlishaw, 1998; Rose and Fedigan, 1995; Treves, 1998) may be explained by the following functional explanation. When a group contains a mix of sexes, age classes and safe and vulnerable individuals, group size does not adequately measure individual predation risk (Treves, 2000).

Females are thought to face a greater risk of predation due to their smaller size. However, previous research in primates finds that males are the more vigilant sex (Baldellou & Henzi, 1992; van Schaik & van Noordwijk, 1989; Steenbeek et al., 1999). There is a relationship in this study that shows females spend a great proportion of time predator vigilant when compared to males. Although a weak relationship it may suggest that females in this study site face a greater risk of predation. Evidence for this may be provided by the observation that there is a higher rate of predation on females at this site. Similarly, Isbell (1990) data suggests that females are targets of a large proportion of total attacks, behind only that of juveniles.

Several animal species have the ability to assess and behaviourally influence the risk of being preyed upon in ecological time (Lima & Dill, 1990). One such environmental characteristic that potentially influences an animal's perceived risk of predation is the density of vegetation and distance to predator refugia. Giving up densities may be costly in that the avoided areas could have valuable resources and highlights a trade-off between resource acquisition and lowing predation risk. The general trend is in contrast to those of Jaffe and Isbell (2009) who found that vervets were less vigilant in open habitat. In this study, individual vervets were more vigilant when they were away from trees and shrubs and the overall position of the group in low vegetation density increased the proportion of scans that recorded predator vigilance. The open habitat lowers an animal's perceived risk of predation as it offers greater visibility and protection from stealth attacks. Cowlishaw (1998) reports that leopards are more successful at low ambush distances, and hunting success increases with more cover. This suggests that, for environments with ambush predators, the probability of predator attack should be a positive function of the level of ground cover. At this field site however, there is an absence of leopard but the presence of cheetah. The open habitat in this case might be more dangerous because cheetah, caracal and jackal do not pose a threat in trees and the cheetah specifically excels at hunting in open habitat. Additionally, this open habitat increases the amount of time necessary to reach the safety of trees. There was also some suggestion that individuals increase vigilance when in a tree or a shrub rather than on the ground. These results suggest that vervet's perceived risk of predation varies according to the predator species in their environment and that they may use the height provided in trees and shrubs to scan the environment before foraging on the ground below. A future analysis should examine the activities used in these areas to establish the influence of habitat on activity patterns.

Predation has been reported to influence the use of the home range in a number of ways. A recent example of this is Willems and Hill, (2009b), finding that vervets will avoid areas that are high in perceived risk of predation at the cost of energy intake. What remains to be determined however is whether there is an immediate change in behaviour following an encounter. Vervet monkeys are prone to numerous predators, regardless of their location within the environment. Therefore efficient anti predator strategies that reduce the overall risk of predation while maximizing the time available for day to day activities, such as energy intake, should be reinforced. Consequently, animals that are slow to return to homeostasis following an encounter may unnecessarily increase the individual costs associated with predation.

Against my predictions, the study animals did not increase their speed nor change their overall direction of travel following encounters with any predator guild, regardless of vegetation density. These results require a further explanation. In the case of aerial predators, Willems and Hill (2009b) argue that they monitor areas much larger than the ranges of their primate prey, and together with their ease of travel and unpredictable use of space over time, results in an even distribution of risk within the horizontal plane over a prey's home range. Additionally, vigilance appeared to be an effective means of detecting an aerial predator well before the vervets were at any risk of attack (pers. obs). This anti-predator strategy allows for vertical substrate adjustment (Willems & Hill, 2009b), rather than changing the direction or speed of travel horizontally.

Table 6 suggests that, at this field site, the chance of coming in contact with a predator is independent of vegetation density. Along with avian predators, snakes and the land predator community that exists here are capable of attacking in dense and open type habitats. In other words, the overall rate of encountering a predator may be equivalent throughout the field site. Therefore instead of increasing speed or changing direction of travel, it may be more appropriate, as a result of the predator species in the area, to continue on with daily activities after the predator has left the area.

The pervasive influence of predators on prey behaviour follows from the fact that an animal's behavioural options that maximize energy intake, access to mates, and regulation of temperature, often expose it to an increased risk of predation (Lima & Dill, 1990). As a result animals must be able to balance the use of anti-predator behaviour with the maintenance of other necessary activities. Prey that have a relatively high escape success, such as vervets, should be able to gather the information on predation risk required to forage actively out of refugia whenever risk is temporarily low (Sih, 1992) and employ anti-predator strategies when there is a sudden increase in risk. The employment of anti-predator strategies which exceed what is necessary to reduce the risk of predation, is an unnecessary use of time and should be selected against.

The results of this study also point to troop size at Samara being larger than expected simply on the basis of resource availability or the risk of predation. Predation risk does not appear to influence space use to any significant degree. Rather than employing more costly anti-predator strategies, the vervets found here increase vigilance in high risk areas. This level of perceived risk is correlated with the distance to safety.

The use of vigilance, along with the absence of leopards and predatory baboons may explain the lack of local extirpations that have happened in other field sites.

Arguably, the most viable explanation for the large troop sizes found here is that successful troop fission, which would offer the benefits of shorter day ranges and IBIs, requires the maintenance of access to the riparian woodland and this is likely to manage only rarely, given that this habitat is saturated. Fission away from the river is likely only to occur when conditions are good and when, historically, temporary water sources are available for colonization. Interestingly, in this regard, following unusually high rainfall and improvements in resource availability during 2011, our two study troops have shown increased dispersion, with small subgroups foraging and, occasionally, sleeping independently within the home range (unpublished data). While it might be argued that subgroups of this kind could simply carve out territories within the larger home range and establish themselves in this way at any time, the high D values mean that any putative subgroup will intersect with other troop members frequently, making it difficult to sustain coherence in membership, especially since social coherence is reduced in these large groups in any case (Henzi et al., in prep.). Given this, the unusually high levels of home range overlap appear to be a natural corollary of what is, in effect, a super-saturated riparian population, sustained by high yields from a few food sources. If this is correct, these populations of vervets should undergo fission events in phases of improved ecological conditions when the areas around artificial water points can support small groups, at least temporarily.

In summary, as at Amboseli prior to the population crash, which in many regards resembles Samara most closely, the fact that *Acacia* provides a consistent source of food products and is very abundant, allows the vervet population to reach high densities in an otherwise inhospitable environment. Unlike Amboseli and other localities, the narrow riparian distribution of *Acacia* and the sharp transition to marginal habitat, makes it very difficult for troops to divide into smaller units. These large river-centred troops, in addition to any implications they carry for conservation in the region, offer an excellent opportunity to study the social dynamics of larger male and female cohorts under natural conditions and in the absence of any obvious ecological stressors.

REFERENCES

Altmann, J. (1974). Observational study of behaviour – sampling methods. *Behaviour, 49,* 227-267.

Anderson, C.M. (1986). Predation and primate evolution. *Primates, 27,* 15-39.

Baldellou, M. (1992). Implications of the multimale troop structure in vervet monkeys (*Cercopithecus aethiops pygerythrus*). PhD. thesis, University of Natal.

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

Barrett, A.S. (2004). *Foraging ecology of the Vervet Monkey (*Chlorocebus aethiops*) in Mixed Lowveld Bushveld and Sour Lowveld Bushveld of the Blydeberg Conservancy, Northern Province, South Africa.* MTech. dissertation, University of South Africa.

Barrett, A.S. (2009). *Spatial and temporal patterns in resource dispersion and the structure of range use and coexistence in a social omnivore* Chlorocebus aethiops. PhD thesis, University of South Africa.

Bercovitch, F.B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour*, 36, 1198-1209.

Bolter, D.R., & Zihlman, A.L. (2003). Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans. *Journal of Zoology, 260,* 99-110.

Borries, C., Larney, C., Lub, A., Ossib, K., & Koenig, A. (2008). Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. *Behaviour Ecology, 19*, 1186-1191.

Broadbent, D., Broadbent, M. (1988). Anxiety and attentional bias: state and trait. *Cognition and Emotion, 2,* 165-183.

Brown, L.R, & Bredenkamp, G.J. (1994). The phytosociology of the southern section of the Borakalalo Nature Reserve, South Africa. *Koedoe, 37,* 59–72.

Chapman, C., & Fedigan, L.M. (1984). Territoriality in the St Kitts vervet, Cercopithecus-Aethiops. *Journal of Human Evolution, 13 (*8*),* 677-686.

Chapman, C., Fedigan L.M., & Fedigan, L. (1988). Ecological and Demographic Influences on the Pattern of Association in ST. Kitts Vervets. *Primates, 29(*3*),* 417-421.

Cheney, D.L. (1980). Intergroup Encounters among Free-Ranging Vervet Monkeys. *Folia Primatologica*, 35(3) 1981.

Cheney, D.L., & Seyfarth, R.M. (1989). Redirected aggressions and reconciliation among vervet monkeys, Cercopithecus-Aeithiops. *Behaviour, 110*, 258-275.

Clutton-Brock, T.H., & Harvey, P.H. (1977). Primate ecology and social organization. *Journal of Zoology, 183,* 1-39.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour. 131*, 293–304.

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

Cowlishaw, G. (1998). The role of Vigilance in the Survival and Reproductive Strategies of Desert Baboons. *Behaviour,* 135, 431-452

Crook, J.H., & Gartlan, J.S. (1966). Evolution of Primate Societies. *Nature, 210,* 1200-1203.

David, H.A. (1988). *The method of paired comparisons*. London: C Griffin.

Dunbar, R.I.M. (1996). Determinants of group size in primates: a general model. *Proceedings of the British Academy, 88,* 33– 57.

Edgar, M.A. (1989). Predator vigilance and group size in mammals and birds: A criticial review of the empirical evidence. *Biological Review, 64,* 13-33.

Enstam, K.L., & Isbell, L. (2007). The guenons (genus *Cercopithecus)* and their allies: behavioral ecology of polyspecific associations. *Primates in perspective* (ed. by

C.J. Campbell, A. Fuentes, K.C. Mckinnon, M. Panger and S.K. Bearder), pp. 252–274. Oxford University Press, New York, NY.

Gould L, Fedigan LM, Rose LM. (1997). Why be vigilant? The case of the alpha animal. *International Journal of Primatology, 18,* 401–414.

Hall, K.R.L., & Gartlan, J.S. (1965). Ecology and behaviour of the vervet monkey, *Cercopithecus aethiops*, Lolui Island, Lake Victoria. *Proceedings of the Zoological Society of London*, 145, 37-56.

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

Harrison, M.J.S. (1983). Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: Seasonal defense of local food supplies. *Behavioural Ecology and Sociobiology, 12,* 85-94.

Harrison, M.J.S. (1985). Time budget of the green monkey, *Cercopithecus sabaeus*: Some optimal strategies. *International Journal of Primatology, 6,* 351-376.

Henzi, S.P. & Weingrill, T. (1998). Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. *Animal Behaviour, 55*(6), 1421-1428.

Hill, R.A., & Dunbar, R.I.M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour, 135,* 411-430.

Hill, R.A., & Lee, P.C. (1998) Predation risk as an influence on group size in ceropithecoid primates: implications for social structure. *Journal of Zoology, 245,* 447-456.

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

Hoffman, M.T., Carrick, P.J., Gillson, L., & West, A.G. (2009). Drought, climate change and vegetation response in the succulent karoo, South Africa. *South African Journal of Science, 105,* 54-60.

Hooge, P.N., & Eichenlaub, B. (1997). Animal movement extension to ArcView. ver. 1. Anchorage, AK, USA: Alaska Science Center - Biological Science Office, U.S. Geological Survey.

Isbell, L.A. (1990). Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aeithiops*) due to leopard predation in Amboseli National Park, Kenya. *American Journal of Primatology, 40*, 41-52.

Isbell, L.A. (1994). Predation on Primates: Ecological Patterns and Evolutionary Consequences. *Evolutionary Anthropology, 3*, 61-71.

Isbell, L.A., Cheney, D.L., & Seyfarth, R.M. (1991). Group fusions and minimum group sizes in vervet monkeys. *American Journal of Primatology 25*, 57-65.

Isbell, L.A., Cheney, D.L., & Seyfarth, R.M. (2002). Why vervet monkeys (*Cercopithecus aethiops*) live in multimale groups. In: Glenn, M.E. and Cords, M. (eds), *The Guenons: Diversity and Adaptation in African Monkeys*. Kluwer Academic/Plenum Publishers, New York, pp. 173-187.

Isbell, L.A. & Young, T.P. (1993a). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour, 45*, 1233-1235.

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

Jack, K.M. (2001). Effect of male emigration on the vigilance behavior of coresident males in white-faced Capuchins (*Cebus capucinus*). *International Journal of Primatology, 22*, 715–732.

Jaffe, K.E., Isbell, L.A. (2009). After the fire: benefits of reduced ground cover for vervet monkeys (Cercopithecus aethiops). *American Journal of Primatology, 71*, 252-260.

Kaghira, J.M., Ngotho, M., Thuita, J.K., Maina, N.W, & Hau, J. (2007). Hematological changes in vervet monkeys (*Chlorocebus aethiops*) during eight months' adaptation to captivity. *American Journal of Primatology, 69*, 1053–1063.

Kent, M., & Coker, P. (2008). *Vegetation description and analysis: a practical approach*. Belhaven Press.

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

Korstjens, A.H., Verhoeckx, I.L., & Dunbar, R.I.M. (2006). Time as a constraint on group size in spider monkeys. *Behavioural Ecology and Sociobiology, 60*, 683–694.

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

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

Lee, P.C., & Hauser, M.D. (1998). Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. *Journal Animal Ecology*, *67,* 347-358.

Lima, S.L. (1992). Life in a multi-predator environment: some considerations for anti-predatory vigilance. *Annales Zoologici Fennici, 29,* 217-226

Lima, S.L., & Dill, L.M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology, 68,* 619-640.

McDougall, P., Forshaw, N., Barrett, L., & Henzi, S.P. (2010). Leaving home: responses to water depletion by vervet monkeys. *Journal of Arid Environments*, *74,* 924-927.

Mitani, J.C., & Rodman, P.S. (1979). Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioural Ecology and Sociobiology*, *5,* 241-251.

Nakagawa, N. (1999). Differential habitat utilization by patas monkeys (*Erythrocebus patas*) and tanalus monkeys (*Cercopithecus aethiops tantalus*) living sympatrically in northern Cameroon. *American Journal of Primatology, 49,* 243-264.

Pruetz, J.D.E. (2009). *The Socioecology of Adult Female Patas Monkeys and Vervets in Kenya.* Pearson Prentice Hall, New Jersey.

Pulliam, H.R. (1973). On the Advantages of Flocking. *Journal of Theoretical Biology 38,* 419-422.

Puth, L.M., & Wilson, K.A. (2001). Boundaries and Corridors as a Continuum of Ecological Flow Control: Lessons from Rivers and Streams. *Conservation Biology, 15,* 21-30.

Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L., & Kie, J.G. (2007). Home range tools for ArcGIS. (http://blue.lakeheadu.ca/hre/)

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

van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour, 87,* 120-144.

van Schaik, C. P. & van Hooff, J. (1983). On the ultimate causes of primate social systems. *Behaviour, 87,* 91-117.

van Schaik, C.P, van Noordwijk, M.A., Warsono, B., & Sutriono, E. (1983). Party size and Early Detection of Predators in Sumatran Forest Primates. *Primates, 24*(2). 211-221.

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

Seyfarth, R.M., Cheney, D.L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour, 28(*4*),* 1070-1094.

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist, 5,* 1052-1069.

Skead, C.J. (1987). *Historical mammal incidence in the Cape Province: Volume 2 - The eastern half of the Cape Province, including the Ciskei, Transkei and East Griqualand*. Dept. of Nature and Environmental Conservation of the Provincial

Administration of the Cape of Good Hope (Cape Town, Republic of South Africa).

Skinner, J.D., & Cimimba, C.T. (2005). *The Mammals of the Southern African Subregion*. University of Pretoria Press.

Smith, E.P., Orvos, D.R., Cairns, J. (1993). Impact Assessment Using the Before-After-Contol-Impact (BACI) Model: Concerns and Comments. *Canadian Journal of Fisheries and Aquatic Sciences. 50,* 627-637.

Stanford, C.B. (1991). Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata). American Journal of Primatology 25,* 35-47.

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

Struhsaker, T.T. (1967a). Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology 48*, 891-904.

Strusaker, T.T. (1967b). Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour, 29,* 83-121.

Tchoukanski, I. (2010). ET Geo Wizards. Version 10.0 for ArcGIS. (http://www.ian-ko.com)

Tichý, L., Rolocek, D., Zeleny, C., & Chytry, M. (2007). New stopping rules for TWINSPAN. European Vegetation Survey, 16th Workshop, March 22-27, 2007.

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

Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour 60*, 711-712.

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

Turner, T.R., Anapol, F., & Jolly, C.J. (1997). Growth, development and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology, 103*, 19-35.

Vermeij, G.J. (1982). Unsuccessful Predation and Evolution. *The American Naturalist, 120 (*6*),* 701-720.

de Vries, H, Stevens, J., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour, 71* (3), 585-592.

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

Welp, T., Rushen, J., Kramer, D.L., Festa-Bianchet, M., & de Passille, A.M.B. (2004). Vigilance as a measure of fear in dairy cattle. *Applied Animal Behaviour Science*, *87,* 1-13.

Whitten, P.L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology, 5,* 139-159.

Whiten, A., Byrne, R.W., & Henzi, S.P. (1987). The behavioural ecology of mountain baboons. *International Journal of Primatology, 8,* 367-388.

Willems, E.P. (2007). *From space to species: Integrating remotely sensed information on primary productivity into investigations and systems models of vervet monkey (*Cercopithecus aethiops*) socio-ecology*. PhD. thesis, Durham University.

Willems, E.P., & Hill, R.A. (2009a). A critical assessment of two species distribution models: a case study of the vervet monkey (*Cercopithecus aethiops*). *Journal of Biogeography, 36,* 2300–2312.

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

Wolfheim, J.H. (1983). *Primates of the World: Distribution, Abundance and Conservation*. University of Washington Press, Seattle and London.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*, 262-300.

Wrangham, R.W. (1981). Drinking competition in vervet monkeys. *Animal Behaviour, 29,* 904-910.

Wrangham, R.W., & P.G. Waterman. (1981). Feeding Behaviour of Vervet Monkeys on Acacia tortilis and Acacia xanthophloea: With Special Reference to Reproductive Strategies and Tannin Production. *Journal of Animal Ecology, 50 (*3*)*, 715-731.