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Population density, spatial dynamics and territoriality in vervet monkeys

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POPULATION DENSITY, SPATIAL DYNAMICS AND TERRITORIALITY IN VERVET MONKEYS

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ABSTRACT

Vervet monkeys (*Chlorocebus pygerythrus*) are generally described as a territorial species, though variations in territoriality have been observed. This research examined the impact of high population density, large group sizes and extensively overlapping home ranges on the expression of territoriality in a population of vervet monkeys. Over a period of eighteen months, data were collected on three large troops of vervet monkeys ($PT_N = 31$, $RBM_N = 39$, $RST_N = 57$) on the Samara Game Reserve, South Africa. I examined the spatial dynamics demonstrated in this population, assed the extent and use of home range overlap and examined the occurrence of intertroop encounters in relation to mate defence, resource defence and home range defence. The home ranges of the troops in this study population overlap substantially, and overlap areas are exploited extensively. The frequency of occurrence of intertroop encounters does not increase in the mating season, nor is there evidence of the defence of particular food patches or home range defence. The findings from this thesis emphasize the importance of examining the expression of territoriality of a population within the context of its environment.

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LIST OF ABBREVIATIONS

I.D. = Identification

ITE = Intertroop encounter

M = Mean

MCP = Minimum Convex Polygon

N = Sample size

PT = Picnic Troop

RBM = River Bend Mob

RST = River Side Troop

SD = Standard deviation

Chapter 1: Introduction

The central focus of this research is the expression of territoriality in an old world primate species: the vervet monkey (*Chlorocebus pygerythrus*). I aim to examine the extent of territoriality and territorial behavior in a population of vervet monkeys living in the semi-arid karoo biome in South Africa. I use data from free-ranging vervets to test predictions regarding the expected display of territoriality in relation to various factors, such as the degree of home range overlap, population density, and occurrence of intertroop encounters (ITEs).

1.1 Home Ranges

An animal's home range is defined as the area it traverses regularly and uses to meet its needs for survival and reproduction over a particular time period (Burt, 1943; Markham, Guttal, Alberts, & Altmann, 2013). The patterning of range use is influenced by a variety of environmental and social variables, including the presence of conspecifics, habitat structure and the density of predators (Harrison, 1983; Mitani & Rodman, 1979). However, it has been argued that, in primates, it is foraging requirements that have the largest impact (Mitani & Rodman, 1979). The home range sizes, extent of home range overlaps and day journey lengths of primate groups are strongly associated with diet type, with home range size being negatively correlated with habitat quality and resource availability (Butynski, 1990; Harrison, 1983). This distribution and availability of resources is suggested to explain the spatial and temporal differences in use of home ranges within a species (Harrison, 1983).

1.2 Intraspecific Competition

Competition exists when any ecological requirement for the success and survival of a population exists in a quantity lower than the optimal amount for the number of individuals that exploit it (Brown, 1964). Competition can arise over mates, food resources, sleep sites and any other resource that is in short supply (Brown, 1964). As competition theory states, the greater the overlap of the use of a resource that is in short supply, such as a limited number of sexually receptive females or limited access to fruiting trees in frugivorous primates, the greater the competition for the resource (Butynski, 1990). Intraspecific (within species) and interspecific (between species) competition has thus often been measured by dietary overlap (Butynski, 1990). The intensity of this intraspecific competition is negatively correlated with the availability of resources, and directly dependent on the density of the population (Brown, 1964). Agonistic behaviour often results from competition, but is not necessary for competition to exist (Brown, 1964).

1.3 Home Range Overlap and Intraspecific Density

An overlap zone is an area of overlap of home ranges of neighbouring conspecific groups (Wrangham, Crofoot, Lundy, & Gilby, 2007). Overlap zones are exploited by two or more groups and are frequently under-used, thus reducing the carrying capacity of the habitat (Wrangham et al., 2007). In a homogeneous environment, where resources are evenly dispersed, animal foraging efforts should be evenly spread, and all areas used equally (Wrangham et al., 2007). In reality, habitats are not entirely homogeneous and overlap zones are rarely used evenly, either in terms of even use by a single troop across its entire home range, or even use by overlapping troops (e.g., spider monkeys (*Ateles geoffroyi*), Chapman (1990), Shimooka (2005); redtail monkey (*Cercopithecus ascanius*), Lambert (1999); chimpanzee (*Pan troglodytes*), Stanford (1995)).

Three hypotheses have been proposed as to why these areas may be so extensively underused. First, overlap zones may be underused due to resource scarcity in these areas (Wrangham et al., 2007). Second, primates have a tendency to return to the centre of their home ranges and, thus, underuse of overlap zones may simply be because regions of overlap are located on the periphery of home ranges (Wrangham et al., 2007). Last, as extensive home range overlap increases the probability of encountering groups, animals may avoid overlap areas if encounters with neighbouring troops involve intense aggression and high risk of injury (the risk hypothesis: Wrangham et al., 2007). However, in habitats with high intraspecific density, where resource competition is higher, overlap areas are theoretically much more likely to be exploited (Butynski, 1990; van Schaik, 1983, Wrangham, Gittleman, & Chapman, 1993).

1.4 Territories

While some species manage intraspecific competition by developing various means of negotiating shared space, other species opt to maintain territories from which conspecific competitors are excluded. A territory is defined as an individual or group's home range, where the boundaries are defended from intrusion by conspecifics (Carpenter, 1987; Maher & Lott, 1995; Markham et al., 2013; Nemtzov, 1997; Nice, 1941; Noble, 1939). Accordingly, the degree of territoriality can be measured by the extent to which an animal's home range does not overlap with the home range of another animal (Grant, 1993; Markham et al., 2013; Nemtzov, 1997; Wilson, 1975). Intraspecific territoriality is often viewed as a means of reducing competition for valuable or limited resources, and is thus indicative of intraspecific competition (Brown, 1964; Butynski, 1990). Territorial defence can be quantified through both the frequency and intensity of intertroop encounters (ITEs: Grant, 1993).

Brown's (1964) theory of territoriality states that territoriality will occur where resources are limited, but will only be expressed if the limited resource is economically defendable (Brown, 1964; Butynski, 1990). For a resource to be economically defendable, the energy expended defending the resource must be less than the energy saved by gaining exclusive access to said resource (Brown, 1964; Butynski, 1990). Further, territories themselves must be defendable, meaning that an animal or group of animals must be able to monitor the boundaries of territories to detect intrusion of conspecifics (Mitani & Rodman, 1979). For territoriality to be expressed, territories should, therefore, not exceed a size where a species can no longer monitor its boundaries, and resources should be both limited and defendable (Butynski, 1990).

1.4.1 Costs and Benefits of Territory Maintenance and Territoriality

The ability of a group of animals to defend its territory is directly related to the quality and distribution of ecological resources within the territory, as well as competition for the resources (Carpenter, 1987; Davies & Houston, 1984; Vlasman & Fryxell, 2002). Territories must be small enough to defend, but large enough to ensure access to a sufficient amount of resources for reproduction and survival (Vlasman & Fryxell, 2002). The theory of optimal territory size rests on the assumption that the costs of defending a territory will increase as the size of the territory increases; thus defended territories will be smaller then undefended home ranges (Grant, Chapman, & Richardson, 1992; Schoener, 1983). This prediction, however, does not hold true for all primate species. When resources are highly abundant or evenly distributed, an individual may waste more energy defending resources than an individual who ignores conspecifics (Grant, 1993).

Territoriality, and boundary defence, depends in part on the ability of the resident troop to detect intruders (Hamilton, Buskirk, & Buskirk, 1976). Mitani and Rodman (1979) hypothesize that territorial defence will only be expressed when the day range of a troop is great enough to allow frequent monitoring of territory boundaries and the location of neighbouring groups. The index of defendability measures the ratio of daily path length to the area of the home range of an animal (Mitani & Rodman, 1979). Assuming that a circle approximates the animal's home range, the index value indicates the number of diameters of the home range that can be crossed per day (Mitani & Rodman, 1979). A large index value (> 1) implies that an animal can frequently encounter range boundaries at various points along the perimeter of its home range, and thus its home range boundaries are defendable (Mitani & Rodman, 1979). Primate species with an index of 1.0 or greater have the capacity to be territorial, but may not express territorial behaviour, while those with an index below 1.0 tend to be non-territorial species that lack the ability to sufficiently patrol home range boundaries (Mitani & Rodman, 1979).

The costs and benefits of maintaining particular territory boundaries are also affected by temporal changes in the distribution and availability of resources, as well as the intraspecific and competitor density in a given area (Grant, 1993; Markham et al., 2013; Schoener, 1983; Vlasman & Fryxell, 2002). For instance, in regions of high primate density, where the population is considered to be at carrying capacity, territoriality has been suggested to emerge as a means of optimizing the use of an area given the intensity of competition (Butynski, 1990; Hamilton et al., 1976). When conspecific density is low, encounters and interactions with competitors are infrequent, and thus the benefits of defence are also low (Grant, 1993). Yoshiba (1968) found that langur (*Presbytis entellus*) groups in low-density populations did not defend areas, while groups in high-density populations did. Similarly, baboons, while generally not described as a territorial species, express territorial behaviour when exploitable habitat is restricted, population density is high and resources are unevenly distributed between troop home ranges (Hamilton et al., 1976). Density does also appear, however, to reach an upper threshold, where territory defence becomes uneconomical due to the increasingly high costs of defending boundaries against conspecifics (Grant, 1993). Territoriality is therefore expected to peak at an intermediate population density (Grant, 1993).

1.4.2 Variations in Territoriality

Despite these expectations, and the balance of costs and benefits of defence, the territoriality that has evolved in a particular species does not ensure consistent territorial expression (Brown, 1964). Variable costs and benefits affect the scale of home range overlap, and degree of territoriality, demonstrated by multiple social groups in a population through time (Chapman & Fedigan, 1984; Markham et al., 2013). To maximize fitness, the degree of territoriality exhibited by an animal, or a group of animals, may be adjusted with changing conditions of the local, inhabited region (Davies & Houston, 1984; Nemtzov, 1997; Vlasman & Fryxell, 2002). As the quality and distribution of resources, particularly food, vary greatly across different habitats, intraspecific variation in territoriality is common (Butynski, 1990; Lott, 1984; Markham et al., 2013; Nemtzov, 1997).

1.5 Intertroop Encounters

The spatial dynamics of a particular population, comprised of multiple social groups, is the product of competition for resources, and the associated fluidity of home range and territory boundaries (Markham, Alberts, & Altmann, 2012). The spatial patterning of groups, and degree of territoriality, are also affected by occurrence of ITEs. ITEs result when members of a social group cooperate to defend resources and prevent intrusion of neighbouring group members, across home range boundaries (Crofoot & Gilby, 2012). A higher frequency of ITE occurrence is often associated with high degrees of territoriality, limited resources and high population density, and thus ITE occurrence is often used as a measurement of territorial behaviour (Harrison, 1983). However, regardless of whether or not a troop actively defends a home range, as per the classical definition of territoriality, intergroup aggression in the form of ITEs still occurs in most primates (Fashing, 2001). The occurrence of ITEs in other contexts, such as mate defence or food patch defence, may therefore appear to indicate territoriality where territorial behaviour is not actually being expressed (superficial territoriality).

1.5.1 The Strategies of Primate Males and Females in ITEs

Males and females are predicted to employ different strategies during ITEs, based on different limitations to reproductive success (Trivers, 1972). As Trivers (1972) hypothesized, male reproductive success is limited by access to mates while female reproductive success is limited by food, and thus males are predicted to defend mates, while females are predicted to defend food resources within their home ranges (Cooper, Aureli, & Singh, 2004; van Schaik, Assink, Salafsky, & Hamilton, 1992). Several hypotheses, highlighting the different strategies of males and females, seek to explain why intertroop aggression occurs in primate species. The first explanation for intergroup aggression is related to male mate defence, where males actively participate in ITEs, directly defending females and excluding extragroup males (Fashing, 2001). Second, direct male defence, where males drive off conspecifics, also functions to protect food resources within the territory, thus benefiting females (Fashing, 2001). Third, males may aid in territorial defence, directly defending food resources and gaining reproductive access to females that fall within that territorial boundary (Fashing, 2001; Wrangham, 1980). The last hypothesis for why intergroup aggression occurs is related to female food resource defence, which is predicted to occur in female bonded primates (Wrangham, 1980). Females are expected to respond aggressively to females from neighbouring troops and cooperatively defend food resources within their territories (Cooper et al., 2004; Fashing, 2001). These various hypotheses are neither an exhaustive list nor are they mutually exclusive. They do, however, highlight the fact that males across most primate species do directly or indirectly defend reproductive access to females (Fashing, 2001).

Despite the presence of male aggression in the occurrence of most ITEs, defending food resources, and competition for food generally, is imperative for many species of primates, and has important implications for social behaviour, dominance relationships, dispersal patterns and group sizes in primates (Chapman & Rothman, 2009). Spatial defence is favoured when specific locations reliably, and continuously, provide food (Kavanagh, 1981). However, in many species, ITEs occur without being directly related to the location of valuable food resources (Wrangham, 1980). In these species, inter-group competition over resources may be occuring indirectly, as groups defend territory boundaries against neighbouring groups, and thus compete for all resources within the defended area (Wrangham, 1980).

1.5.2 Core Versus Peripheral Defence

Some primate groups defend core regions of their home ranges whereas others more frequently defend peripheral areas (Brown 2013). Those species that participate in peripheral defence are generally territorial, and aggressively defend home range boundaries. Those species that participate in core defence interact with neighbouring troops throughout their home range, but are more likely to be aggressive and expel intruders while in the core of their home ranges (Brown, 2013). While the reasons for these differences in defence are not fully understood, it has been suggested to be a consequence of differences in the availability of food in the core and periphery, making one or the other more critical to defend (Brown, 2013). Brown (2013), however, could not confirm this suggestion in her study of grey-cheeked mangabeys (*Lophocebus albigena*) and redtail monkeys (*Cercopithecus ascanius*), finding evidence for neither core nor peripheral defence associated with food availability. Instead, it appeared that both species were participating in food patch defence.

1.5.3 The Impact of Intertroop Encounters on Patterns of Space Use

Frequency of ITE occurrence has been shown to influence spatial separation of groups and spatial overlap of home ranges (Markham et al., 2012). In a study of wild baboons (*Papio cynocephalus*), those troops that lost an ITE experienced short term costs, using the area surrounding the ITE less intensely than previously (Markham et al., 2012). Few data exist on the impact of the occurrence of a single

ITE on the spatial and behavioural patterns of primate groups. Most data are presented or analyzed at a much larger temporal scale.

1.6 Vervet Monkeys

Vervet monkeys (*Chlorocebus pygerythrus*) are a medium sized, semi-arboreal, semi-terrestrial African primate. Vervets live in troops ranging from a mean size of 12.1 to 33.0 individuals (Pasternak et al., 2012). Vervet troops have been reported to travel through their home ranges as cohesive units, rarely subgrouping (Harrison, 1983). Troop spread has, however, been shown to vary considerably as a consequence of variations in habitat structure, the effects of specific behavioural activities, and food availability (Harrison, 1983). Vervet population densities range from 4.3 to 86.4 km^2 (Pasternak et al., 2012), excluding our study population, and between- and within-group competition can occur at very high rates (Cheney & Seyfarth, 1987).

Vervet monkeys have long been considered a territorial species, where both adult males and females rigorously defend fixed territory boundaries during and outside of the mating season (Cheney & Seyfarth, 1987; Cheney, 1981; Isbell, Cheney, & Seyfarth, 1991; Struhsaker, 1967). Vervets females are philopatric and are thus expected to be active in aggressive ITEs (Wrangham 1980). However, this argument rests on the assumption that high-quality food will be distributed in defendable patches, which is not often the case for this omnivorous primate (Willems, Barton, & Hill, 2009). Further, vervet monkeys, as with several other species of old world primates, inhabit large, diverse regions of the African continent (Wolfheim, 1983), and intraspecific variation in territorial expression has been observed (Chapman & Fedigan, 1984). In a review of fifteen *Chlorocebus* field studies by Chapman and Fedigan (1984), ten studies classified their study population as highly territorial, two classified their population as mildly territorial and two demonstrated no evidence of territoriality (one further study gave no indication of degree of territoriality).

Vervet monkeys in the Masai-Amboseli Game Reserve in south-central Kenya had territory boundaries that were reported to shift over time, but rarely overlapped (Struhsaker, 1967). Other study sites have reported some degree of home range overlap (Harrison, 1983), which contradicts the strict notion of territorial behaviour. Within the *Chlorocebus* genus, particularly extensive variation exists; *C. tantalus* in Cameroon have been reported to merge without agonism (Kavanagh, 1981), while *C. sabaeus*, inhabiting the Caribbean island of St. Kitts, exhibits very mild territorially (Chapman & Fedigan, 1984), and *C. pygerythrus* in Kenya exhibits intensely aggressive intertroop interactions and territorial defence (Struhsaker, 1967). This extensive variation has led researchers to describe the genus as exhibiting facultative territoriality, or differing degrees of territoriality in response to different ecological constraints (Chapman & Fedigan, 1984; Kavanagh, 1981). Averages of territorial behaviour cannot, therefore, be taken across populations nor can they be considered as binary constructs (Lawes & Henzi, 1995). The expression of territoriality in a population should instead be investigated within the context of the population's habitat, as well as its structure and density.

1.7 Research Aims

While there has been a good deal of research on territoriality and competition, much less exists on the variability of intraspecific territoriality, and the factors that lead to the diverse expressions of territoriality. Species are often placed into behavioural categories representing the average, instead of acknowledging intraspecific variation (Chapman & Rothman, 2009; Lawes & Henzi, 1995). As Chapman and Rothman (2009) state, it is important to understand and emphasize intraspecific variation, and the magnitude of this variation across lineages. Primate social structure, and arguably the expression of territoriality, is a combination of adaptation to modern environmental constraints and phylogenetic inertia (Chapman & Rothman, 2009).

1.7.1 Study Population

The population of vervet monkeys that I studied, inhabits narrow riparian corridors in the semi-arid South African Karoo (Pasternak et al., 2012). The area beyond this narrow corridor is largely inhospitable and incapable of sustaining vervet populations, unless man-made water sources are present. Despite the fact that this population is geographically restricted, the population has been reported to sustain group sizes that far exceed those previously reported, and inhabit extensively overlapping home ranges (e.g., Fedigan, 1988; Struhsaker, 1967b). Figures 1.1-1.3 indicate home range sizes, home range overlap and mean troop sizes of five vervet study populations across the African continent, including earlier data (2010-2011) from the study population examined in this thesis.

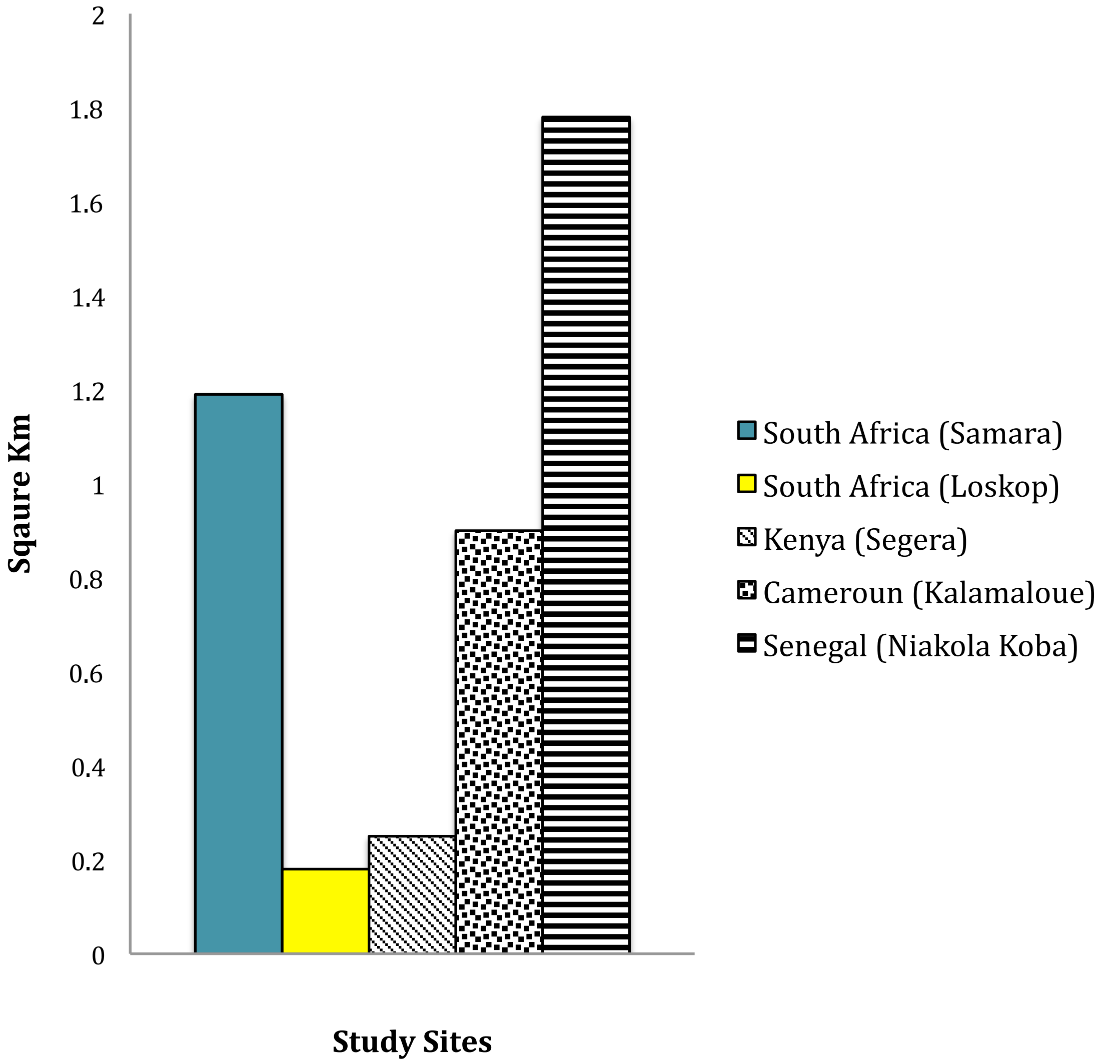

Figure 1.1. Mean home range sizes of five study populations across the African continent; South Africa (Samara) (Pasternak et al. 2012), South Africa (Loskop) (Barrett, 2004, 2009), Kenya (Segera) (Enstam & Isbell, 2007; Pruetz, 2009), Cameroun (Kalamaloue) (Nakagawa, 1999; Willems, 2009) and Senegal (Niakola Koba) (Harrison, 1983, 1985). The Samara sight indicates data from the 2010-2011 field season, and the same study population investigated in this thesis.

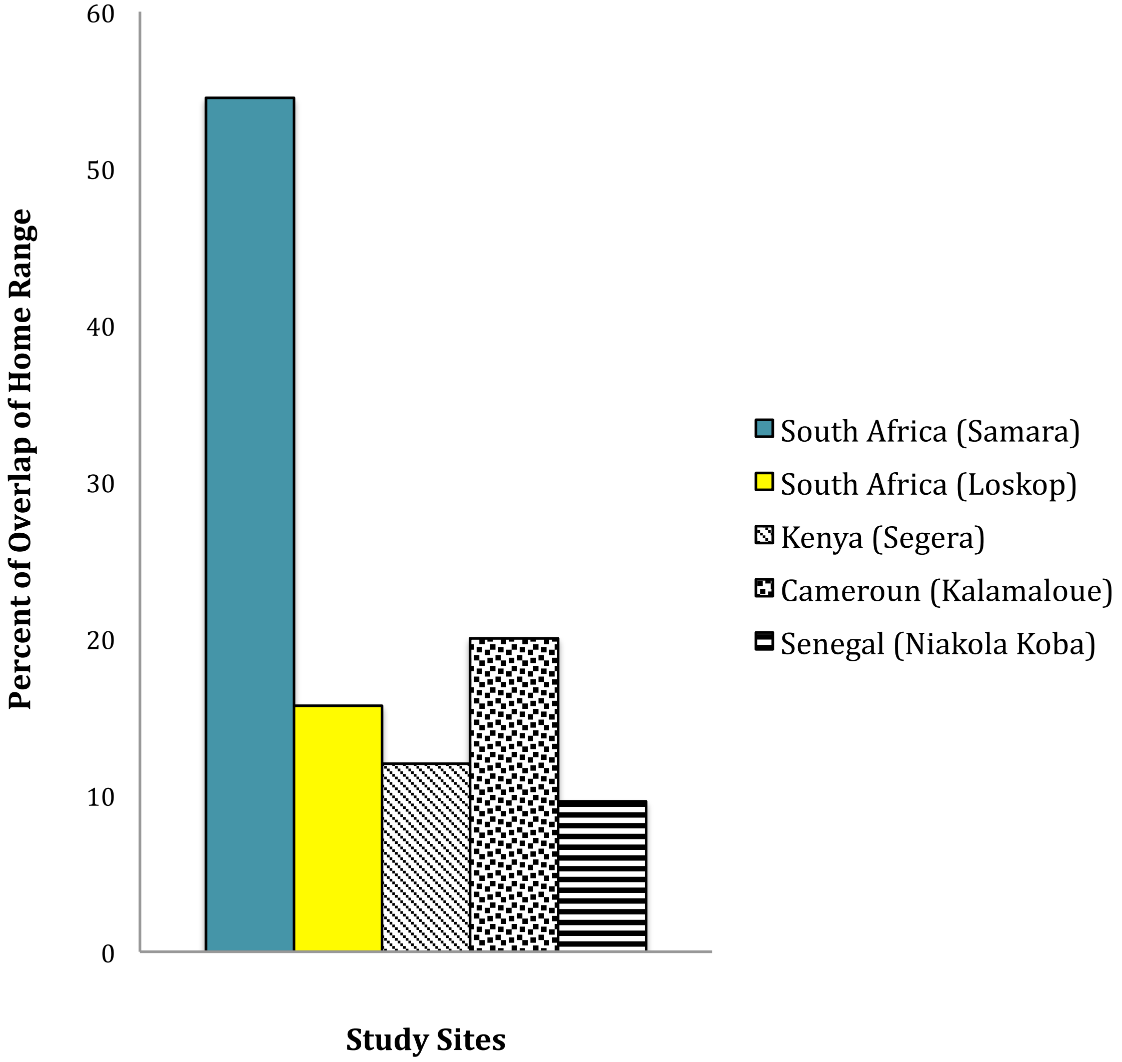

Figure 1.2. Mean percent of overlap of home ranges of five study populations across the African continent; South Africa (Samara) (Pasternak et al. 2012), South Africa (Loskop) (Barrett, 2004, 2009), Kenya (Segera) (Enstam & Isbell, 2007; Pruetz, 2009), Cameroun (Kalamaloue) (Nakagawa, 1999; Willems, 2009) and Senegal (Niakola Koba) (Harrison, 1983, 1985). The Samara sight indicates data from the 2010-2011 field season, and the same study population investigated in this thesis.

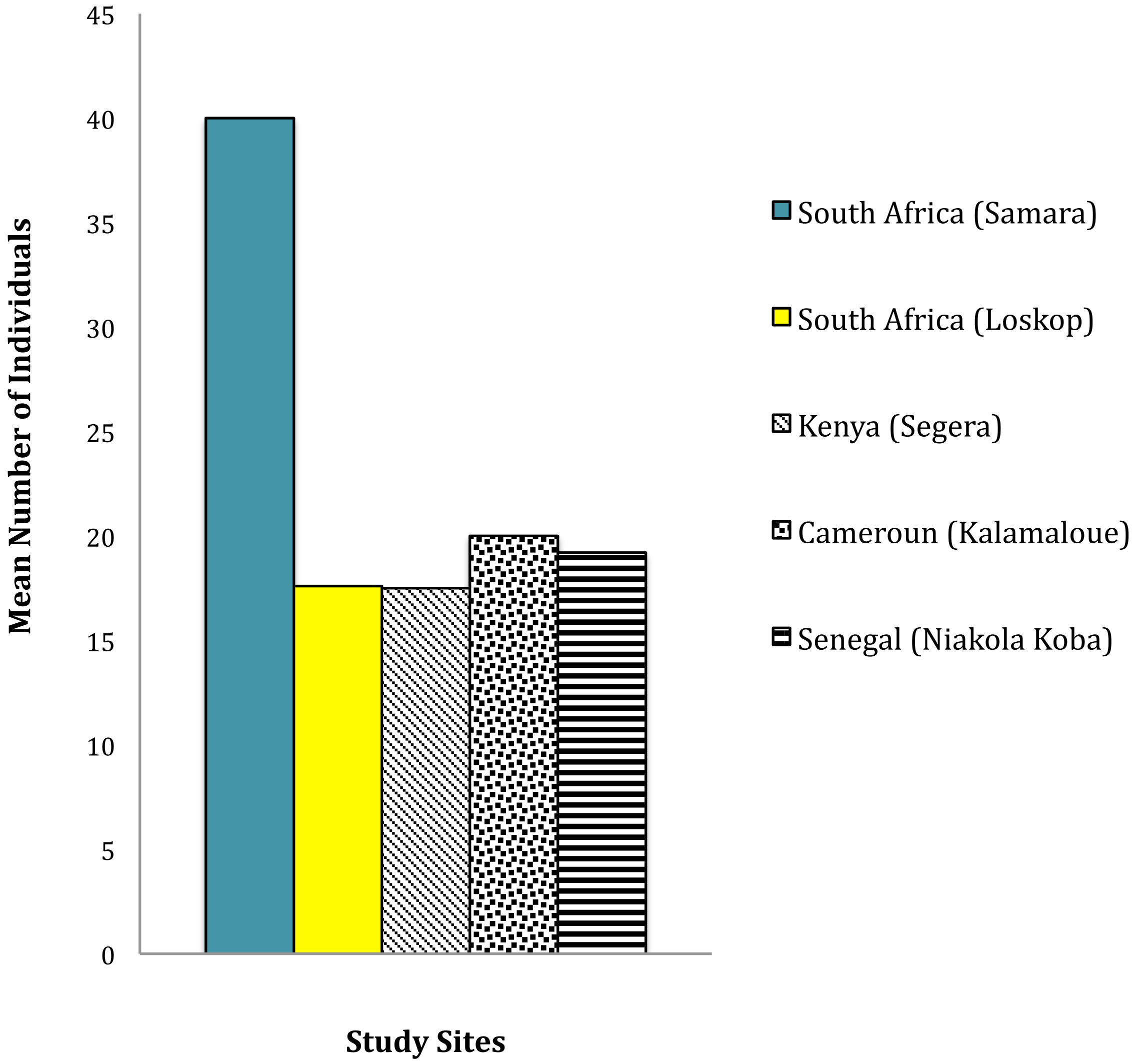

Figure 1.3. Mean troop sizes of five study populations across the African continent; South Africa (Samara) (Pasternak et al. 2012), South Africa (Loskop) (Barrett, 2004, 2009), Kenya (Segera) (Enstam & Isbell, 2007; Pruetz, 2009), Cameroun (Kalamaloue) (Nakagawa, 1999; Willems, 2009) and Senegal (Niakola Koba) (Harrison, 1983, 1985). The Samara sight indicates data from the 2010-2011 field season, and the same study population investigated in this thesis.

The Samara study population is distinctive for its large troop sizes and extent of home range overlap, both of which are clearly much more extensive then the other study populations displayed in Figures 1.2-1.3. Despite these large troop sizes and home range overlap, home range sizes are comparable to other populations, further emphasizing the density of this study population (Figures 1.1). While vervet monkeys are generally characterized as being highly territorial, the extensively overlapping home ranges previously reported for this population contradict the notion of what it means to be territorial. The study troops are clearly not excluding conspecifics from their home ranges. However, despite this, they are known to interact aggressively with one another (Freeman, 2009), with ITEs, ranging from mildly antagonistic to fiercely agonistic (Takahashi, 2012), occurring frequently (Freeman, 2009). How, then, is territoriality expressed in a population that does not fit the parameters of any particular theoretical framework, or the characteristics of any previously described population of this species?

The aim of this study was to examine the extent of territoriality exhibited in this population of vervet monkeys. First, I examined the spatial characteristics of this population and its implications for territorial behaviour. Second, I examined the occurrence of ITEs in time and space, and their impact on intratroop cohesion and intertroop dominance hierarchies. Third, I compared the extent of territoriality indicated by these data with previous observations on this population. Previous studies took place when environmental conditions were less favourable then the data discussed in this thesis, in particular water was scarce and resources were less abundantly available.

1.7.2 Specific research aims for this thesis:

1. Describe the spatial characteristics of this population.

a) Examine the extent of home ranges, and temporal fluctuations in home range size in relationship to neighbouring troops.
b) Assess the extent of overlap between the home ranges of neighbouring troops.
c) Assess the degree of use of these areas of overlap.
a) Compare the frequency of use of shared versus exclusive space.

2. Examine the occurrence of intertroop encounters (ITEs).

a) Assess the frequency of ITE occurrence.
b) Determine if troops are defending food resources, mates and/or space.
c) Examine the location of ITE occurrence in relation to the core of troop home ranges and regions of extensive overlap.
d) Describe the impact of ITE occurrence on the spatial cohesion of a troop, and the spatial patterns of movement of the troop as a whole.

1.7.3 Hypotheses

1.7.3.1 Areas of Overlap

I will examine the areas of home range overlap displayed across the three study troops. While the definition of territoriality infers that no overlap in home ranges exists, home range overlap has been reported previously in this study population (Pasternak et al., 2012). Following these results, I will examine the use of these overlap areas.

I aim to test the following hypotheses regarding use of overlap areas:

i) In previous studies overlap areas have been reported to be used less extensively for a variety of hypothesized reasons than those areas occupied exclusively by a troop (Wrangham et al., 2007). I hypothesize that the vervets will spend less time in areas of overlap than those areas not shared with neighbouring troops (i.e. exclusive space).

1.7.3.2 Intertroop Encounters

Intertroop encounters (ITEs) have been previously reported to occur frequently across this study population (Freeman, 2009). It is evident that intertroop competition exists within this population, but what exactly these troops are attempting to defend remains undetermined. Most commonly, primates have been reported to defend food resources, mates or mating access and home range space (Fashing, 2001). I will investigate frequency of ITE occurrence across the study period, and its relation to the mating season. Following these results, I will examine the spatial location of ITE occurrence, and its relation to foraging sites and home range boundaries. Previous studies of this population have shown that the troop home ranges are economically defendable, according to Mitani & Rodman's defendability index (1979), and thus territoriality is able to be expressed (Pasternak et al., 2012).

I aim to test the following hypotheses regarding ITE occurrence and resource defence in this population:

i) Large territories have been suggested to be maintained in order to exclude neighbouring groups from mating opportunities within the territory (Brown, 1964). If males in this population of vervet monkeys are participating in mate defence or access to mates, I hypothesize that the frequency of ITE occurrence will increase significantly in the mating season, compared to the remaining months of study.

ii) If seasonal shifts between the rainy/summer season and the dry/winter season resulted in differences in the availability of resources, we would expect a shift in the competition for resources, with higher intra and interspecific competition occurring in the winter. I hypothesize that the number of observed ITEs will increase in the winter season, as competition between neighbouring groups increases.

iii) This population of vervets has been reported to rely heavily on *Acacia karroo* products (Pasternak et al., 2012), which are readily and consistently available to all three study troops. I hypothesize that vervet monkeys are not defending particular food patches and thus there will be no correlation between the location of ITEs and regions of high foraging density.

iv) Primates have been reported to more actively defend core regions of their home range, as oppose to peripheral areas (Markham et al., 2012). If vervets are displaying low levels of territorial behaviour, I hypothesize that troops will avoid confronting neighbouring troops in peripheral areas, preferentially defending the core areas which are most heavily exploited and thus presumably the most valuable for troop success.

v) If they do not display a pattern of mate defence or food patch defence, vervet troops may be competing with neighbouring troops for all resources within their home ranges (Wrangham, 1980). If vervets are seeking to defend their home ranges, I hypothesize that ITEs will occur more frequently in the periphery of troop home ranges than in core areas.

vi) If troops are not actively seeking out one another, and as extensive regions of overlap of home ranges exist in this population, I hypothesize that ITEs will more frequently occur in regions of extensive overlap of highly used areas, where the probability of encountering neighbouring troops is high.

Lastly, I aim to test the following predictions regarding the impact of ITE occurrence on the spatial dynamics of individual troops and the population:

vii) During ITEs, male vervet monkeys have been reported to herd females of their own group, while females have been reported to form intragroup coalitions against neighbouring groups (Cheney, 1981). I therefore hypothesize that ITEs will affect the spatial cohesion of the study troops, with the extent of troop spread decreasing after ITEs.

viii) I predict that the trajectory of troop movement will be altered by the occurrence of ITEs, with troops deflecting significantly from their original paths.

Chapter 2: Subjects, Study Site and Methods

2.1 Subjects

2.1.1 Taxonomic Affiliation

The genus *Chlorocebus*, comprised of six species including the vervet monkey (*Chlorocebus pygerythrus)* and eight subspecies, is the most geographically widespread and most abundant genus/group of African monkeys, alongside the baboons (Cawthon Lang, 2006; Struhsaker, 1967c; Wolfheim, 1983). Until recently, vervet monkeys, along with their sister taxon, the patas monkeys (now *Erythrocebus patas*), were classified as *Cercopithecus*, along with the other guenons (Groves, 2001; Groves, 2004; Tappen, 1960; Wolfheim, 1983). The guenon clade diverged from the mangabey, baboon and macaque groups approximately 10 million years ago, as suggested by molecular and fossil evidence (Cords, 1987). Radiation across the African continent has lead to diversification, though reproduction isolation between many species has not yet been attained (Cords, 1987; Tappen, 1960).

While the molecular evidence remains unclear (Disotell, 1996), vervet and patas were taxonomically separated from the guenons due largely to morphological differences (Groves, 2004). Further, vervets are semi-arboreal, semi-terrestrial animals, enabling them to exploit a wide range of habitats, while guenons are more commonly tree-dwellers, often restricted to forested regions (Fedigan & Fedigan, 1988). The literature, however, remains unclear about the taxonomic designation of vervets, with papers labeling vervets as *Cercopithecus aethiops* (Isbell, Young, Jaffe, Carlson, & Chancellor, 2009), *Chlorocebus aethiops* (Bolter, 2011), and *Chlorocebus aethiops pygerythrus* (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013), among others. The common name vervet has also been used to describe both the particular species (*Chlorocebus pygerythrus)*, and the genus *Chlorocebus* as a whole. While the taxonomy remains contentious, for the purpose of this thesis, the classification described by Groves (2001) was used as well as the term vervet to describe the species (*Chlorocebus pygerythrus)* (Figure 2.1).

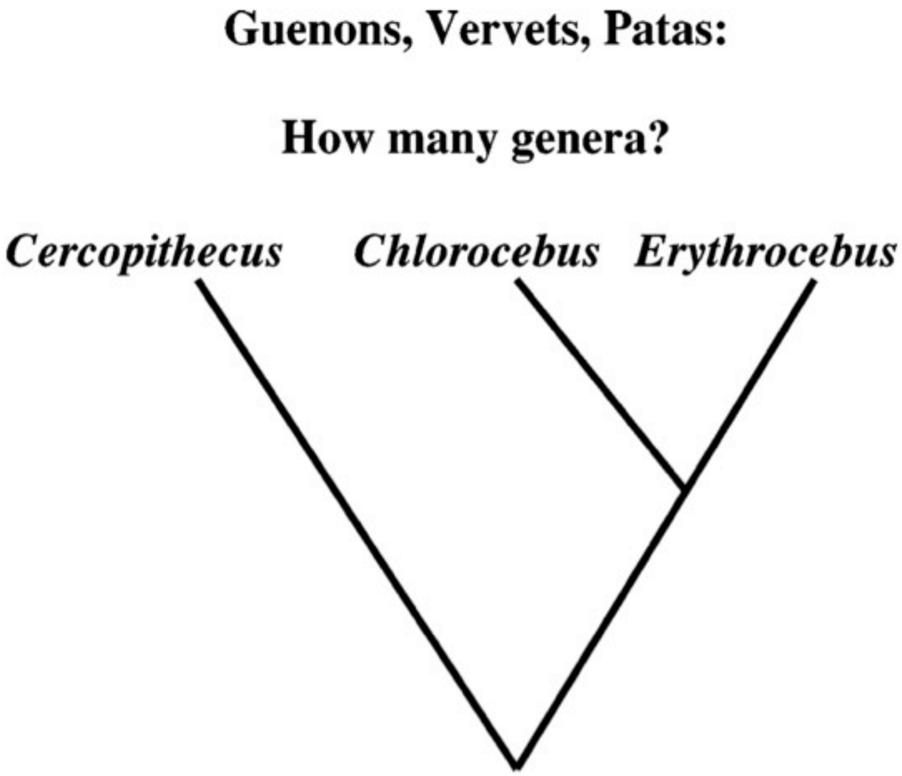

Figure 2.1. Cladogram displaying the relationship between guenons (*Cercopithecus*), vervets (*Chlorocebus*) and patas (*Erythrocebus*), and the current, but contentious, separation of genera (from Groves, 2004).

2.1.2 Physical Features

Vervet monkeys are small bodied to medium bodied primates, with grey coats of fur and black faces, framed with white hair. Abdominal skin is blue and covered by light white and grey fur. Both adult females and males have coloured genitalia, which are more clearly visible in the adult males with their blue scrota and red penises. The colouring is not as marked in adult females, who are instead generally recognizable in the field by their protruding nipples (Figure 2.2). There is visible, though only moderate, sexual dimorphism with adult males weighing between 3.9 and 8.0 kg, averaging 5.5 kg, and adult females weighing between 3.4 and 5.3 kg, averaging 4.1 kg (Cawthon Lang, 2006).

Vervet monkeys are seasonal breeders, with the mating season in the southern hemisphere occurring from approximately March to June. Females become pregnant for the first time around the age of 40 months (Turner, Anapol & Jolly, 1997). After a gestation period of 163 days (Fairbanks & McGuire, 1984; Turner, Anapol, & Jolly, 1997), they give birth to a single infant. In the case of the vervet monkey troops under study, females experienced inter-birth intervals of approximately 21 months (RBM = 17.9 months; RST = 24 months), though some were able to give birth in consecutive years (Pasternak et al., 2012).

Figure 2.2. An adult female (left) and an adult male (right) warming in the morning sun.

2.1.3 Distribution

The genus *Chlorocebus*, along with the baboons (*Papio*), is the most common and widely distributed species of non-human primates on the African continent (Struhsaker, 1967b; Tappen, 1960; Wolfheim, 1983). As well as inhabiting large regions of sub-Saharan Africa, *Chlorocebus sabaeus* was introduced to the Cape

Verde islands off the west coast of Africa, and several Caribbean islands in the late 1600s, where they remain today (Cawthon Lang, 2006).

2.1.4 Ecology and Habitat

Vervets are semi-terrestrial, with the amount of time spent arboreally or on the ground being determined by the structure of the local habitat (Figure 2.3) (Fedigan & Fedigan, 1988). In subsaharan Africa, vervets inhabit savannahs, woodlands and dry forests (Isbell & Young, 1993; Wolfheim, 1983). While most commonly found along riparian zones of savannas, vervets exploit a wide variety of environments, including open and marginal habitats (McDougall et. al., 2010; Struhsaker, 1967; Fedigan & Fedigan, 1988). Vervet monkeys do, however, require sleeping trees within their home range, both as refugia and as sleeping sites (Fedigan & Fedigan, 1988). Further, unlike forest dwelling primates, vervet monkeys require direct access to water, although they are capable of surviving without such access for extended periods (McDougall et. al., 2010).

Figure 2.3. A troop of habituated vervet monkeys exploiting a relatively open landscape, dominated by *Acacia karroo,* on the Samara Private Game Reserve.

2.1.4.1 Diet

Vervet monkeys are opportunistic omnivores, with their diet consisting mainly of plant species and invertebrates (Barrett, Brown, Barrett, & Henzi, 2010; Harrison, 1984; Struhsaker, 1967). In many regions, species of acacia tree, such as *Acacia xanthophloea, A. karroo, A. caffra* and *A. tortilis*, are the most important food source for vervets (Barrett et al., 2010; Lee & Hauser, 2012; Pasternak et al., 2012; Struhsaker, 1967). Acacia trees are a constant source of food throughout the year, providing gum, flower buds, pods and leaves for consumption. Species of grasses, herbs and fungi are also major components of a vervet's diet (Lee & Hauser, 2012; Struhsaker, 1967). The vervets at Samara, South Africa, foraged on 26 different plant species and fungi, and frequently consumed insects, most notably grasshoppers and termites (Pasternak et al., 2012).

2.1.5 Home Range Defense and Territoriality

Home range use and troop ranging patterns are greatly affected by shifts in spatial and temporal resource availability, most notably in the dry season when resources are less readily available (Barrett et al., 2006; Barrett et al., 2010; Harrison, 1983). Similarly, the size of a vervet group's home range and territory is not related to group size, but varies with the distribution of vegetation of the region, and the availability of resources (Pasternak et al., 2012; Struhsaker, 1967). In Struhsaker's (1967) study of Amboseli vervets, home range sizes spanned from 0.18 km^2 to 0.96 km^2. Barrett et al.'s (2010) study of vervet monkeys in the Loskop Dam Nature Reserve, South Africa, revealed much larger home range sizes of 1.38 km^2 for one study group, and 2.24 km^2 for the second.

Vervet monkeys are described as a territorial species; actively defending against intrusions from neighbouring groups (Isbell, Cheney, & Seyfarth, 1990; Isbell & Young, 1993; Struhsaker, 1967). Vervet troops, however, frequently encroach into neighbouring group home ranges when total available resources decrease and when numbers of conspecifics increase, decreasing the available amount of food sources per individual (Isbell et al., 1990).

2.1.5.1 Movement Patterns

Vervet troops tend to remain together for the duration of the day, traveling and foraging as a cohesive unit (Struhsaker, 1967). Vervet troops have, however, been frequently observed to divide into sleeping subgroups at night, and regroup after sunrise the following day (Struhsaker, 1967). The distance traveled by a troop in a single day is largely dependent on the productivity of the habitat, and varies greatly between groups. Struhsaker's (1967) observations of two groups of vervet monkeys showed great variation in the daily distance traveled by each group, and the average distances traveled by each group, with one group traveling an average of 1431m in a day, and the other traveling an average 936 m in a day. Harrison's (1984) study of a closely related species, *Chlorocebus sabaeus*, revealed similar day journey lengths and variations: varying between 665m and 2670m.

2.1.6 Social Organization and Behaviour

Vervets live in multi-male, multi-female troops ranging in size from 5 to 76 individuals, with an average size of approximately 25 (Fedigan & Fedigan, 1988). Vervets are female philopatric, with females remaining in their natal groups, and males dispersing at maturity (Henzi & Lucas 1980, Cheney 1981, Fedigan & Fedigan, 1988). Males generally migrate repeatedly during their lives, and there is evidence that arrivals and departures peak during the breeding season (Cheney, 1981; Freeman, 2009; Henzi & Lucas, 1980). Males reach puberty and become reproductively mature between the ages of 4 and 5 years, marked by the development of adult canines, an increase in muscle mass and behavioral changes (Bolter, 2011; Fairbanks & McGuire, 1985). Females reach subadulthood between the ages of 30 and 36 months, and commence copulating, giving birth to their first infant around the age of 4 (Bolter, 2011; Turner et al., 1997).

Both sexes have a clear dominance hierarchy (Baldellou & Henzi, 1992; Bramblett & Bramblett, 1982; Struhsaker, 1967). Female dominance remains largely stable across time, while male dominance fluctuates with the emigration and immigration of males. Vervet monkeys are seasonal breeders, with mating season in the southern hemisphere occurring in the fall, normally beginning in March and ending in June and birth season commencing in the spring and summer, generally stretching from October to February (Henzi & Lucas, 1980).

2.2 Study Site

2.2.1 Location

Field research was conducted on the 270 km^2 Samara Private Game Reserve, in the Eastern Cape Province of South Africa (32 22°S, 24 52°E) (Figure 2.4). The site is located approximately 35 km from the town of Graaff-Reinet in the semi-arid nama karoo. Vervet monkeys are widespread in the region and have been historically documented in this semi-arid biome since at least the 18th century (Skead, 1987). The vervet troops under study inhabit a narrow riparian corridor, centered on the Milk River, in an otherwise arid and inhospitable landscape (Figure 2.8) (Pasternak et al., 2012).

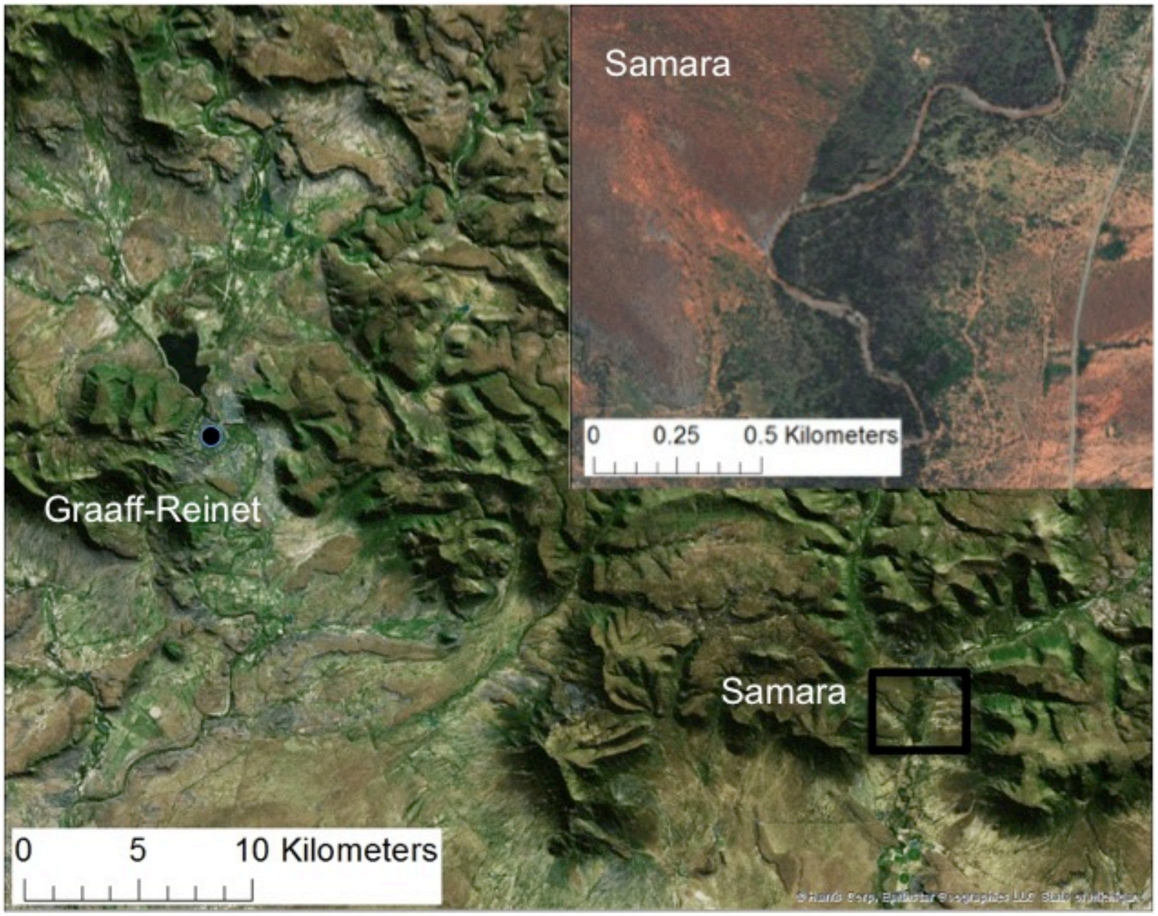

Figure 2.4. The location of the Samara Game Reserve in relation to Graaff-Reinet, South Africa. The inset provides an aerial view of the study area.

2.2.2 Climate and Seasonality

The Samara Private Game Reserve experiences strong seasonality in both temperature and rainfall. The nearest weather station to the Samara field site is located approximately 35 km away, in the town of Graaff-Reinet. Samara is separated from Graaff-Reinet by mountainous terrain and this is likely to have an effect on local climate. Nevertheless, the weather readings from the station do provide an indication of the approximate temperatures, wind speed and precipitation of the region, and the field site. The total annual rainfalls recorded at the Graaff-Reinet weather station during my study were: 309.10 mm in 2011, 298.66 mm in 2012, and 64.00 mm from January through August of 2013 (see Figure 2.5). Unlike earlier years, rainfall occurred fairly consistently throughout the 18-month study period, with no clear wet or dry season, allowing the Milk River to flow continuously (McDougall et. al., 2010).

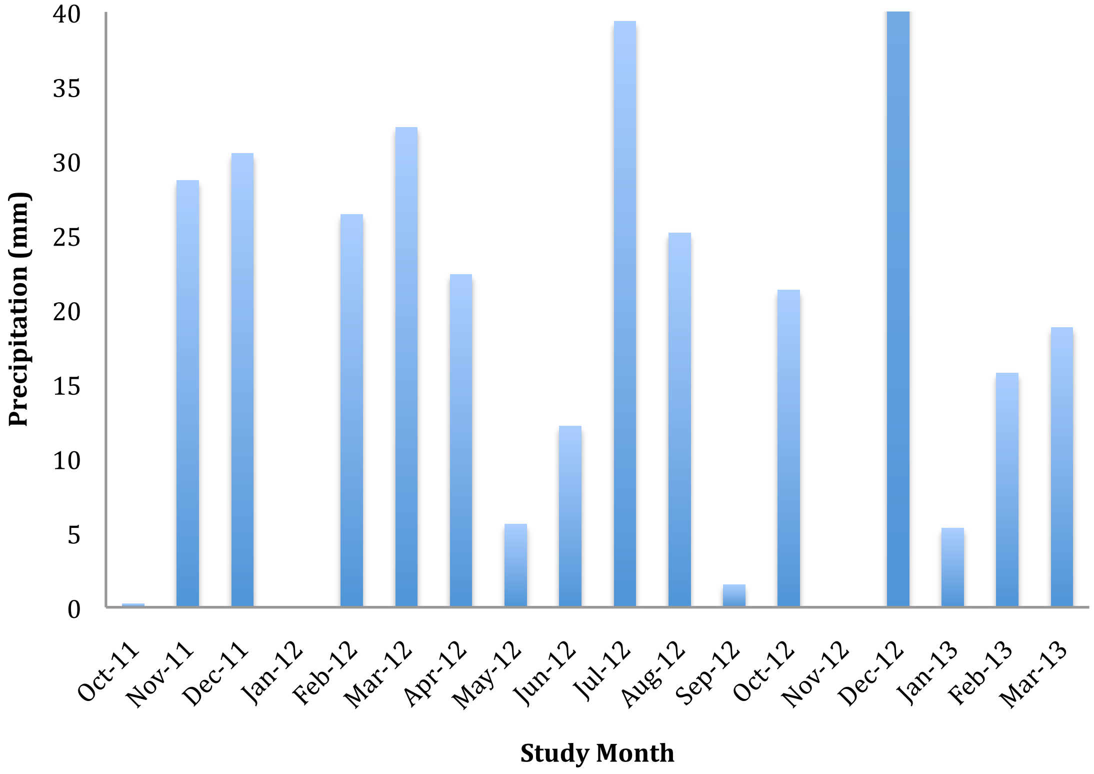

Figure 2.5. Total monthly precipitation in Graaff-Reinet from October 2011 to March 2013 (“Climate in Graaff-Reinet,” 2013).

Temperature ranged from a mean minimum of 9.1 °C to a mean maximum of 24.2 °C. The coldest month was July 2012, with a minimum temperature of 1.6 °C (mean monthly temperature of 9.1 °C), and the warmest month was January 2012, with a maximum temperature of 34.4 °C (mean monthly temperature of 24.2 °C) (see Figure 2.6). Wind speeds remained fairly constant through the course of the year, with a maximum mean wind speed of 12.1 km/h occurring in January 2012 and a minimum mean wind speed of 8.9 km/h in April 2013 (see Figure 2.7). Maximum wind speeds were at their highest in August 2012, reaching sustained speeds of 22.7 km/h.

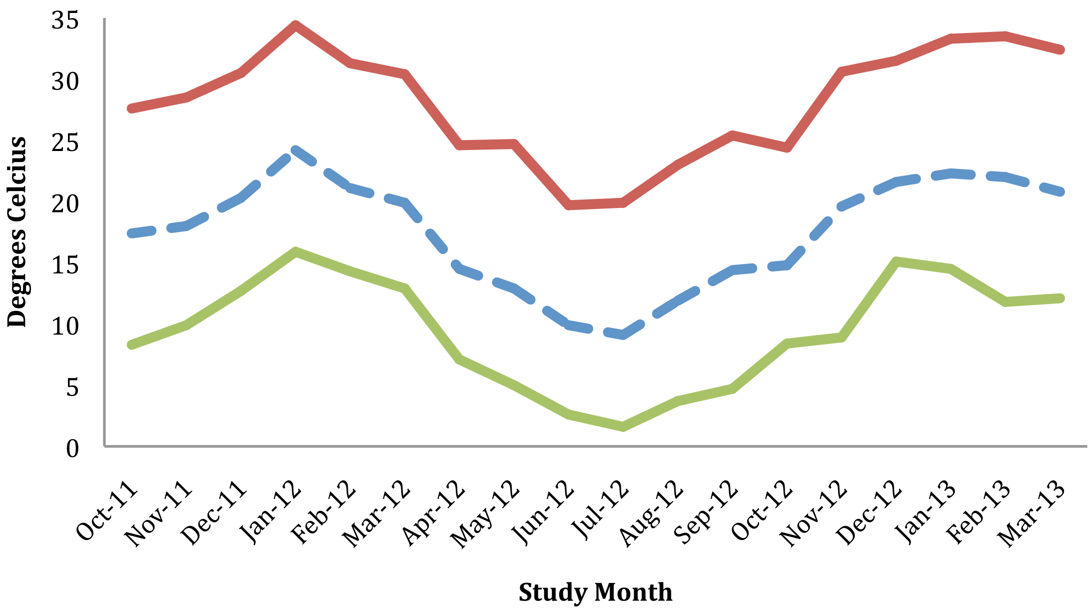

Figure 2.6. Mean monthly temperatures recorded in Graaff-Reinet, from October 2011 through March 2013. The upper line represents the mean maximum monthly temperature. The bottom line represents the mean minimum monthly temperature. The center dashed line indicates the mean temperature ("Climate in Graaff-Reinet," 2013).

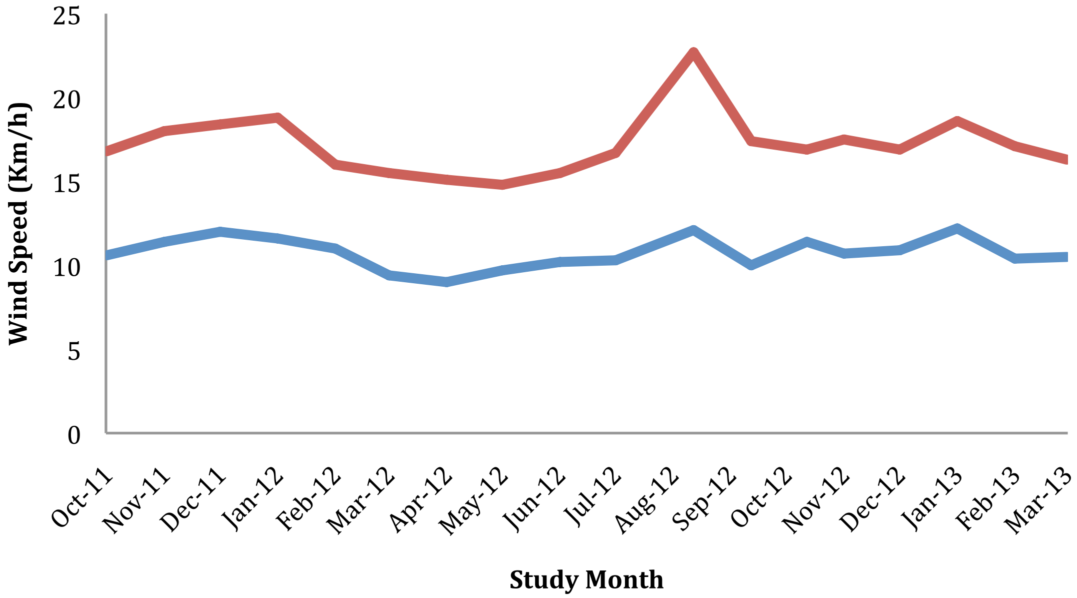

Figure 2.7. Recorded wind speed per month, from October 2011 through March 2013. The upper line indicates the maximum sustained wind speed, and the lower line indicates mean wind speed, in kilometer per hour ("Climate in Graaff-Reinet," 2013).

2.2.3 Flora

The home ranges of the study troops were characterized by relatively low plant species diversity (Pasternak et al., 2012). Pasternak et al. (2012) identified three major plant communities, comprising a total of 124 plant species. These three major plant communities constitute two structural units; open dwarf shrublands and dense *Acacia karroo* woodland (Pasternak et al., 2012).

The largest plant community, occurring along the river and floodplain, is the *Lycium oxycarpum–A. karroo* woodland (Pasternak et al., 2012). The woodland is dominated by *L. oxycarpum* and *A. karroo*, with a heavy presence of *Rhus lancea* trees and *Rhus longispina* shrubs (Pasternak et al., 2012). The regions dwarf shrublands are comprised of *Pentzia globosa–Grewia robusta* to the west, and P*. globosa–Cynodon incompletus* to the east (Pasternak et al., 2012). Both shrub communities are relatively open areas that extend on higher ground from the woodland. While the shrublands are degraded from cultivation and grazing practice that took place prior to 1998, the dense woodland remains in good condition and provides a consistent food source for the large river-centred vervet troops (Pasternak et al., 2012) (Figure 2.8).

Figure 2.8. A troop of vervet monkeys at the Milk River, located at the centre of the Samara field site.

2.2.4 Fauna

There is a wide variety of other large mammals living on the game reserve, including several species of antelope, zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*) and cape buffalo (*Syncerus caffer*). Potential and known vervet land predators include cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*). While aerial predators were rarely spotted, they include martial eagle (*Polemaetus bellicosus*), Verreaux's eagle (*Aquila verreauxii*) and Cape eagle owl (*Bubo capensis*). Perhaps the greatest threat to the vervets are venomous snakes, specifically the puff adder (*Bitis arietans*) and Cape cobra (*Naia nivea*).

2.3 Study Population

Data were collected on three troops of habituated monkeys: Picnic Troop (PT), River Bend Mob (RBM) and River Side Troop (RST). Both RST and RBM have been under observation since 2008, and are very well habituated. Habituation of PT began in January of 2012, with data collection commencing in April, 2012. All adults and sub-adults were individually recognizable by facial features or other identifying characteristics.

Troop sizes are provided in Table 2.9. All three troops were larger than the average group sizes reported for the species, and, therefore, have large adult cohorts (Pasternak et al., 2012). Troop membership fluctuated across each time period; consequently the number of individuals listed reflects the average number of group members per time period. Exact troop counts were very difficult to obtain.

Most often, counts were conducted when a study troop was crossing the Milk River. Counts of RST were rarely obtained during my study period as the troop was predominantly widely dispersed.

Adult female numbers remained relatively constant over the 18-month period, with a largely stable dominance hierarchy. Adult male numbers changed much more frequently across the study periods, with a continuous influx of immigrating males and loss of emigrating individuals, resulting in fluctuations in the male dominance hierarchy across groups. New males immigrating from non-habituated troops became habituated after approximately one month of observation. Data collection began on immigrant males after this one-month period of observation if the male remained consistently present in his new group. Deaths and disappearance of individuals occurred across all age classes in the troops.

Table 2.9. The average number of group members in PT, RBM and RST per time period. No data are available for PT in time period 1.

Troop	Time Period 1	Time Period 2	Time Period 3
PT	*No Data*	35	26
RBM	55	35	27
RST	70	55	45

2.3.1 Troop Spatial Dynamics

Both RBM and PT were generally fairly cohesive. In contrast, RST was frequently divided into two or more sub-groups, each spatially widely separated from the others. Each troop used several different sleep sites across the study periods, occasionally sleeping in separate subgroups in multiple sleep sites or, more commonly, sleeping as a single group but alternating sleep sites regularly.

Observations and analyses by Pasternak et al. (2012) demonstrate average day journey lengths of 2806.3 m with RBM and 2353.6 m with RST. These day journey lengths may be particularly high, however, as the data come from a year of low rainfall, where troops frequently had to travel outside their core areas to a distant water source (Pasternak et al., 2012). RBM's home range covered 1.76 km^2 (99% MCP), with a core area of 0.10 km^2 (Pasternak et al., 2012). RST's home range covered a much smaller area of 0.64 km^2, with a core area of 0.07 km^2 (Pasternak et al., 2012). RBM shared 23 % of their home range with 5 other troops, and RST shared 86 % of their home range with 4 other troops (Pasternak et al., 2012).

2.4 Data Collection

2.4.1 Structure of Observation Times

When possible, the troops were followed from dawn (06:00-09:00) to dusk (17:30-19:00). On all other occasions, troops were followed for ten-hour blocks, varying between a dawn start time and a dusk end time. The time blocks covered each day varied to account for differences in the amount of seasonal sunlight, with over four hours more of sunlight in the summer than the winter. As the data investigated in this thesis are drawn from an 18-month period, the study was divided into three consecutive time periods: October 2011 through March 2012 (summer/time period 1), April 2012 through September 2012 (winter/time period

2) and October 2012 through March 2013 (summer/time period 3). During the first period, data were collected on RST and RBM. The third troop (PT) was added for the second and third periods, during which all three troops were under observation.

2.4.2 Behavioural Observations

Using handheld, GPS-equipped data loggers (Trimble Nomad) and Pendragon Forms software, we collected behavioural data on all adult and subadult vervet monkeys. Subadults, for the purpose of this study, were identified by size and sexual activity (juvenile and infants IDs were not maintained). All animals could be approached to within 1 to 5 meters.

Behavioural observations were collected by instantaneous scan sampling at 30-minute intervals, for a period of 10 minutes. During each 10-minute scan sampling period, data were collected on as many individuals within the study troop as possible (see Table 2.10 for data collected during scans).

Table 2.10. Data collected by scan sampling.

Behaviour	**Definition**
General	
Time Stamp	Time and date when scan was started
Identity	Identity of focal animal
Height	Distance of individual from the ground (ground, <1m, 1-3m, >3m)
Nearest Neighbour	Nearest adult or subadult male and female to the focal animal (estimated distance from focal animal)

Location	
Ground	On the ground, within two meters of shelter (tree, shrub or cliff)
Open	On the ground, greater than two meters from shelter
Tree	Plant species, greater than 1.5 meters in height, with lateral branches supported off the ground
Shrub	Plant species, greater than 1.5 meters in height, with several stems arising near or at the ground
Upper	Exposed at the top of a shrub or tree
Activity	
Foraging	Gathering or eating a food source
Moving	Movement greater than the length of one body (excluding slight movement to resume another activity, such as foraging or grooming)
Resting	Neither foraging, partaking in social activity or moving
Allo-groomer	Grooming individual (I.D. of partner)
Allo-receiver	Grooming recipient (I.D. of partner)
Autogroom	Grooming oneself
Aggression	Direction agonistic behaviour towards another, or receiving agonistic behaviour from another (I.D. of participants)
Other	Engaging in activity that does not fall under the other categories, such as swimming or playing (I.D. of participants when applicable)

2.4.3 Spatial Sampling Techniques

2.4.3.1 Group Location

The relative position of the habituated troops within their home ranges was collected using Pendragon Forms software on GPS-equipped Trimble Nomads, which, assuming open sky, have an accuracy of 2 to 4 meters (determined using Horizontal Root Mean Squared method). A GPS point was taken at the estimated center of the troop at the start of each scan period, at 30-minute intervals. When the study troop was split into separate subgroups, as was often the case with RST, a GPS point was taken at the estimated center of the subgroup under observation, and the identity and members of the subgroup noted.

At times when numerous observers were working with a single troop, several troop centroid points were recorded. In this case, the average of those centroids was taken, leaving a single GPS coordinate at each half hour interval for each troop. After the average centroid at each interval was calculated, where multiple points existed, a total of 7836 GPS points at troop center remained, recorded over 522 days of observation on individual troops; 1730 GPS centroids recorded with PT across 136 days (*M* = 12.72 +/- 8.23 *SD* GPS centroids per day), 2941 with RBM across 186 days (*M* = 15.81 +/- 7.71 *SD* GPS centroids per day), and 2941 with RST across 200 days (*M* = 15.83 +/- 7.87 *SD* GPS centroids per day). All time stamps considered for the analyses were taken from the recorded GPS coordinates, and are in Coordinated Universal Time (UTC).

2.4.3.2 Individual Location

Along with group location, individual spatial data were also collected with RBM and RST. Through the course of a day, between 1 and 4 researchers walked continuously through a single troop of monkeys, recording the spatial location of all adult and sub-adults encountered. Each individual was approached within 1-5 m, and using Pendragon Forms, the animal's spatial location was recorded by GPS point, along with the time stamp, identity of the individual, height of the individual, juveniles within 5 meters and activity of the individual (as defined in Table 2.10). The spatial locations of individuals were recorded as frequently as possible. Over the course of 103 study days (47 days with RBM, 56 days with RST) from November 2011 through July of 2012, we recorded a total of 38,984 GPS points, with 18,968 on RST and 20,016 on RBM.

2.4.4 Intertroop Encounters

The occurrence of intertroop encounters (ITE) was documented on an ad libitum basis during the study period (see Table 2.11). An ITE was defined as any occasion when a troop was within 20 m of another troop, and displayed some form of agonistic behavior, such as vocalisations, head-bobbing and charges. If aggressive behaviour commenced again, separated by a minimum of 10 minutes from the first ITE, then this was scored as a second ITE. Spatial and behavioural data were collected at the beginning of each ITE .

A GPS point was taken as close to the encounter as possible, without interrupting the ongoing interaction between troops. Instances where vervet troops observed one another but did not interact aggressively were not recorded as ITEs, nor was the presence of the other troop recorded.

Table 2.11. Information collected at the beginning of an ITE.

Category	**Definition**
Time Stamp	Time and date when scan was started
Focal Troop	Identity of focal troop
Encounter Troop	Identity of the encountered troop
Distance	Closest distance the focal came within the encounter troop
Participants	Identity of active participants (the individuals who partook in aggressive acts towards the encountered troop)
Others	Identity of individuals located within 25m of the ITE who did not participate

2.4.5 Other Ad Libitum Data Collection

All predation events were recorded, along with the alarm-call response elicited by the vervet monkeys, and, where possible, the identity of the predator. Instances where one animal displaced or supplanted another animal were recorded, along with the identities of the participants, to allow for the construction of dominance hierarchies. In addition to these data, records of all births, deaths and migration events have been recorded since November 2008 on RST and RBM, and since April 2013 on PT.

Group spatial data, behavioural data and ad libitum data were collected by myself, A. Matlock, E. Matlock, N. Ducheminsky, T. Rutherford, J. Parker, N. Collins-Hryciuk and R. McFarland from October 2011 to July 2012, and augmented by data collected from August 2012 through April 2013, by A. Matlock, E. Matlock, R.

McFarland, D. Murphy, K. Roberts, M. Sommerville, J. Jarrett and K. Lucas. Individual spatial data were collected by myself, A. Matlock, E. Matlock, N. Ducheminsky and T. Rutherford, from October 2011 through July 2012.

2.5 Data Analysis

2.5.1 Day Journey Length

Day journey length was calculated for each troop across each time period (1, 2 and 3, as defined in *Structure of Observation Times*), with a total of 49 day journeys calculated with PT, 107 with RBM and 119 with RST. Day journey length was calculated across all study days where a minimum of 10 consecutive hours of data were collected, and where at least ten GPS centroid points were taken. Using the GPS centroid points taken at half hour intervals, distance in meters was calculated from one centroid to the next across each day, on each study troop. Data that were collected beyond the ten hours were not included in the day journey analyses, thus the resulting day journey lengths are a minimum estimate, particularly in the summer months (time period 1 and 3) when daylight extended several hours beyond the ten hour constraint. The distances between centroids on a given day were then added together to give a total daily distance travelled. Day journey lengths are more accurate for those days where a GPS centroid was available at every half hour interval, and where troops were continuously followed from morning sleep site to evening sleep site. However, as start and end points were not consistently available across the 18 month study period, the ten hour and ten centroid limitations were employed.

2.5.2 Home Range Sizes

GPS points taken at half hour intervals were used to determine the home range size, extent and areas of greatest use of the study troops. As previously stated, analysis was divided into 3 time periods (summer/1 = October 2011-March 2012, winter/2 = April 2012-September 2012 and summer/3 = October 2012-March 2013). Data files in Microsoft Excel were imported into ArcGIS 9.3. The kernel density routine in the extension Home Range Tools for ArcGIS was used to calculate the home range extent and areas of high usage of each troop in each given time period. Using an adaptive (Gaussian) kernel with a bandwidth of 40m and a cell size of 10m, minimum convex polygon (MCP) estimates of total home range extent (at 100% MCP), average home range (at 95% MCP) and core area (at 50% MCP) were determined.

2.5.3 Areas of Overlap

Areas of home range overlap for each of the three time periods were calculated using ArcGIS 10.1. Home ranges of the troops at 50% MCP and 100% MCP were overlaid, and areas of overlap (km^2) were extracted.

2.5.4 Use of Overlap Areas

The "simple ratio index" was used to quantify the percent of time spent in a given area:

$$(n/N)*100$$

n refers to the number of records that were taken in a given area, and *N* refers to the number of records that were taken across the total area. To calculate the amount of time spent in regions of overlap, the number of GPS coordinates taken on a single troop that fell within an overlap area was divided by the total number of GPS coordinates taken with that troop across the full extent of its home range.

2.5.5 Defendability Index

According to Mitani & Rodman (1979), the ability of a group of animals to defend a territory depends on the group's ability to monitor the boundaries of the given territory. The defendability of a territory can be predicted by an index of defendability:

$$D = \frac{d}{\sqrt{(4A/\pi)}}$$

where D is the defendability index, d is the mean day journey length (km) and A is the area of the home range (km^2). Territorial species are predicted to have an index value of greater then one.

2.5.6 Frequency of ITE Occurrence

ITEs are often used as a measure for intergroup competition, and thus can provide insight into the types of intraspecific competition and degree of territoriality present in this population. ITE occurrence was documented across the duration of the study period, from October 2011 to March 2013, totaling 522 observation days (136 with PT, 186 with RBM and 200 with RST). The spatial location, time and date of all ITEs was recorded using Pendragon forms. The ID of the focal troop, encounter troop and distance between troops was also recorded. The raw frequency of ITE occurrence across the study period was documented. The number of ITEs per troop is a count of all recorded ITEs when the given troop was a focal troop. ITEs were not included in the count when the given troop was the troop encountered by the focal troop.

2.5.6.1 Frequency of ITE Occurrence by Person Hour

While comparisons across troops using the raw ITE data are valuable and necessary for certain analyses, a ratio of ITEs/person hour was also calculated to correct for additional hours and observers. Frequency of occurrence was measured in comparison to calculated average number of person hours on each given habituated troop. Number of person hours was determined by taking the average of two separate measurements of person hours on the same day.

The first measurement of person hours was determined by subtracting the time of the first recorded GPS coordinate from the time of the last recorded GPS coordinate of a single observer. The given numbers of observation hours of each individual in a single day were added, giving a total number of person hours for each field day, for each troop. This first measurement may potentially overestimate the number of person hours in a given day, as observations may have been suspended, or GPS coordinate intervals missed by observers.

The second measurement of person hours was determined by counting the total number of GPS points recorded by one observer on a single day. GPS points were taken at half hour intervals on each observation day, throughout the course of the 19-month study period. The total number of GPS points taken by all observers on a given day was added and multiplied by 30 minutes, giving a total number of observation hours based on number of GPS points recorded. This second measurement could potentially underestimate the total number of person hours on a given troops, as an observer may have forgotten to record a GPS point at a particular interval, or allowed another observer on the same troop to record the GPS coordinate closer to troop-centre, while still actively observing the troop and recording other data.

To allow for the most accurate and feasible estimate of person hours, an average of the first and second measurement was taken. This average was used to determine a ratio of ITEs per person hour, by dividing the total number of ITEs on each troop, on each study day, by the total number of person hours on the given day.

A ratio for each month was also calculated, by diving the total number of ITEs on each troop, each month (totally 18 study months for RBM and RST, and 12 study months for PT) by the total number of person hours in that same month.

2.5.7 Location of ITE Occurrence

2.5.7.1 Feeding Density

In order to investigate whether the location of ITEs was related to defence of specific food patches, I sought to compare the location of ITEs to the foraging density of the given area. Individual GPS and behavioural data collected with RBM and RST from October 2011 to August 2012 was used to create foraging density maps. I selected the coordinates of all individuals whose activity at the time of observation was foraging, leaving a total of 1913 GPS coordinates for RBM, and 1899 GPS coordinates for RST. The foraging density maps were not divided by time period as no data are available for time period 3.

The GPS coordinates of all foraging individuals were then mapped using ArcGIS 10.1 (ESRI, 2011). In the Spatial Analyst Extension, the kernel density tool was used to interpolate a raster surface, with an output cell size of 5 m. The darkened areas of the resulting surface map represent areas of high foraging density, while the light coloured areas represent regions of low foraging density. The GPS coordinates of all ITEs that occurred with RBM and RST over the same extent of time were then overlaid on to the surface maps. The tool Extract Values to Points (Spatial Analyst Extension) was then used to give each ITE coordinate an associate raster cell value, or value of foraging density derived by the kernel density estimation. One ITE from the focal troop RBM fell outside the extent of the kernel density surface map, and was deleted from the sample. In total, 141 ITEs with RBM and 192 ITEs with RST were spatially matched with their associated foraging density value.

2.5.7.2 Minimum Convex Polygons

The home range of each troop was calculated for the three previously defined time periods, as described above (*2.5.2 Home Range Sizes*). Along with the 50 %, 95 % and 100 % minimum convex polygons (MCPs) used for home range analysis, MCPs were calculated across all 10 % intervals (10, 20, 30, 40, 50, 60, 70, 80, 90, 100), where the core 10 % indicates the area of greatest use. The locations of all

ITEs that occurred with each focal troop, in each time period, were then overlaid on the 10 % MCP home range maps. The ITE map layer was then joined with the home range polygon layer, spatially associating each ITE with a 10 % MCP. The frequency of ITE occurrence in each 10 % MCP could then be determined.

2.5.7.3 Conjoint Probability Index

A high frequency of ITE occurrence in peripheral areas of troop home ranges may simply be due to the fact that the likelihood of encountering neighbouring troops is, in fact, higher in these peripheral areas. Conjoint probability indexes were therefore calculated for areas of home range overlap between study troops. At each time period, the home ranges of each pair of studied troops at 10 % MCP were overlaid, and all but the regions of intersect were removed. This left a map of two overlaid sets of MCPs at 10% intervals, creating new polygons, each with two values of degree of usage by each troop. For instance, a 10% MCP polygon at the center of one troops home range (representing the troops area of highest use) may overlap with the 100% MCP at the outskirts of the second troops home range (representing the troops area of least use). Both these values were retained for each polygon, and when multiplied, provide a value of the probability of finding both troops in each polygon simultaneously.

For each map, describing the overlap of two troops, the coordinates of the ITEs that occurred between those same two troops were overlain. Each ITE coordinate was then spatially matched with its associated conjoint probability index, to determine if ITEs do, in fact, occur in areas of higher probability of encounter.

2.5.8 Troop Spatial Deflection Post-ITE

Spatial deflection post-ITE was examined in order to investigate the effect of ITEs on the spatial patterns of the study troops, and to investigate the possible presence of an intertroop dominance hierarchy, which has been suggested to occur as a means of mediating intertroop competition in dense regions (Hamilton et al., 1976). To determine the angle of deflection following an ITE, our sample was restricted to 154 days where observers were following a minimum of two habituated troops simultaneously (71 days with RBM and RST, 49 days with RBM and PT and 34 days with RST and PT). The sample was then restricted to days where at least one ITE took place between the two observed troops, leaving a total of 50 days where 202 ITEs occurred between simultaneously observed troops.

Using the GPS coordinates taken at half hour intervals and the coordinates of the ITE, I calculated the approach vector of both observed troops (from the troop centroid GPS coordinate to the shared ITE coordinate). The vector of departure from the ITE was calculated between the coordinate of the ITE and the next troop centroid coordinate recorded. The deflection from the trajectory of the approach angle was then determined.

Deflection angles post-ITE were compared to angles of deflection from one troop centroid coordinate to another, to examine if the spatial deflection post-ITE was significantly larger. Deflection angles post-ITE were also compared across troops.

2.5.9 Intratroop Spatial Cohesion Post-ITE

Troop spread post-ITE was estimated in order to better understand the effects of ITEs on the spatial patterns of the members of the study troops. The extent of troop spread was calculated using the GPS coordinates taken of individual adult and sub-adult individuals on a given troop over the course of a day. The spread of troop members on RST and RBM was calculated at half hour intervals across 62 days (29 days with RBM, and 33 days with RST). Analysis was restricted to the days in which at least one ITE occurred when individual data was being collected. Across this sample of days, 22 ITEs occurred with RBM as the focal troop, and 19 ITEs occurred with RST. Using the time stamp of ITE occurrence, the extent of troop spread before and after the occurrence of an ITE was determined. When multiple ITEs occurred within a half-hour interval, the ITEs were reduced to a single instance, and the before and after troop spread selected.

Each analyzed day was divided into half hour intervals, corresponding with the half hour intervals when troop center points were taken (on the hour and half hour). Those individual coordinates that fell within the 30 minutes of each half hour interval were rounded to the nearest half-hour. For example, those individual coordinates taken between 11:46 and 12:15 were rounded to 12:00, and those taken from 12:16 to 12:45 to 12:30. Once the time stamp of each individual coordinate was rounded to the nearest half hour interval, GPS coordinates were converted to UTM to allow for distance to be calculated in meters. The two GPS coordinates, or individuals, that were located the furthest from one another at each interval were determined. The distance between these two coordinates thus determined the total spread of the troop at a given interval.

2.6 Statistical Analysis

Spatial data were stored and organized in Microsoft Excel for Mac 2008, Version 12.1.0 (Microsoft, 2008). All spatial data were mapped and analyzed using ArcGIS 9.3 and 10.1 software (ESRI, 2011). Statistical analysis was conducted using SPSS 21.0 (Corp., 2012).

Chapter 3: Results

In order to assess the degree of territoriality displayed by this population of vervet monkeys, I first describe the use of space by the three habituated troops before I consider the consequences of resource competition and space use on the occurrence of intertroop encounters (ITEs). I then examined the impact of ITEs on the spatial cohesion and patterns of movement of the study troops.

3.1 Day Journey Length

A day's journey length was calculated for all days that the study troop was followed for a period of at least ten hours, and where a minimum of ten half hour troop centroid points were taken. The number of calculated day journeys and the mean and standard deviation of day journey distance are provided in Table 3.1. Speed is given in meters per day, with distance rounded to the nearest 5m to accommodate for measurement error in the GPS receiver.

Table 3.1. The number of calculated day journey lengths and mean and standard deviation of day journey distances for each troop, across each time period. Speed in meters per day is also given.

Troop	Statistic	Time Period 1	Time Period 2	Time Period 3
PT	*N*	*No Data*	14	35
	M		1257.40 m	1278.83 m
	SD		321.45 m	360.74 m
	Speed		1260 m/day	1280 m/day
RBM	*N*	17	48	42
	M	1975.53 m	2089.91 m	1673.14 m
	SD	580.50 m	369.40 m	412.77 m
	Speed	1975 m/day	2090 m/day	1675 m/day
RST	*N*	15	62	42
	M	1932.16 m	1993.74 m	1394.81 m
	SD	629.89 m	622.90 m	335.66 m
	Speed	1930 m/day	1995 m/day	1395 m/day

To assess the difference within and between troops, two mixed-design ANOVAs were performed. The first mixed-design ANOVA was used to assess the difference across all three habituated troops in time period 2 and time period 3, as data are not available for PT in time period 1. All variables were normally distributed. The results of the ANOVA are displayed in Table 3.2. As Mauchly's Test of Sphericity was significant, the Geisser-Greenhouse correction is reported. A significant difference was identified across time period, with RBM and RST traveling further in time period 2 than in time period 3, and PT traveling slightly further in time period 3 than time period 2. There was also a significant difference between troops, and a significant difference of time by troop. Follow-up Dunnett T3 posthoc tests revealed a significant difference between PT and RBM ($p < 0.001$) and PT and RST ($p < 0.001$), but no significant difference between RBM and RST ($p = 0.295$).

Table 3.2. The results of the mixed design ANOVA comparing the day journey lengths of PT, RBM and RST across time period 2 and time period 3.

Time	$F(1, 95) = 37.632$, $p < 0.001$	partial $n^2 = 0.284$
Troop	$F(2, 95) = 22.682$, $p < 0.001$	partial $n^2 = 0.323$
Time period x Troop	$F(2,95) = 8.150$, $p < 0.001$	partial $n^2 = 0.146$

A second mixed-design ANOVA was performed to assess the difference between RBM and RST across all three time periods. All variables were normally distributed. The results of the second ANOVA are displayed in Table 3.3. A significant difference was found across time, but not by troop or for troop by time. Follow-up paired t-tests revealed a significant difference between time period 2 and time period 3 ($p < 0.001$), and between time period 1 and time period 3 ($p = 0.014$) with RBM, as well as time period 2 and time period 3 ($p < 0.001$), and between time period 1 and time period 3 ($p = 0.004$) with RST.

Table 3.3. The results of the mixed design ANOVA comparing the day journey lengths of RBM and RST across all three time periods.

Time	$F(2, 60) = 24.152, p < 0.001$	partial $n^2 = 0.446$
Troop	$F(1, 30) = 0.072, p = 0.790$	partial $n^2 = 0.002$
Time x Troop	$F(2, 60) = 0.142, p = 0.868$	partial $n^2 = 0.005$

While the imposed constraint of a 10 hour day journey length does provide valuable insight into the average daily distance traveled in the winter and summer months, it is important to note that the average day journey lengths provided are an underestimate of the total daily distance traveled. The day journey lengths provided in time period 2 are a reasonable estimate of the actual distance traveled, as daylight hours barely extended beyond the ten hour constraint during the winter months. Day journey lengths in time period 1 and 3, representing the summer months, are much more of an underestimate of the total distance traveled, as daylight hours extended well beyond the 10 hour constraint. Table 3.4 provides the average distance traveled and number of hours extended beyond the ten hour restriction, by troop and time period. As can be seen, day journey lengths often extended beyond the 10 hour constraint imposed for day journey length analysis.

Table 3.4. The average time (hours) and distance (meters), by troop and time period, extended daily beyond the ten hour day journey length constraint.

Troop	Extra Time	Time Period 1	Time Period 2	Time Period 3
PT	Average Time (Hours)	*No Data*	0.30	1.50
	Average Distance (Meters)		30.06	164.72
RBM	Average Time (Hours)	1.12	0.69	1.46
	Average Distance (Meters)	321.22	121.10	172.83
RST	Average Time (Hours)	1.07	0.59	1.48
	Average Distance (Meters)	206.21	110.01	195.83

3.2 Home Range Size

The day journeys were aggregated for each troop and each time period in order to derive an estimate of home range size. Over the 18-month study, RBM averaged 1.81 km^2, RST averaged 1.36 km^2, and PT averaged 1.26 km^2. The areas covered by the 50%, 90% and 100% minimum convex polygons (MCP) are indicated in Table 3.5. Home ranges were calculated using kernel density in ArcGIS software, thus the smaller the MCP value, the more intensely used the area was (i.e. 10% MCP represents the 10% of the home range where the troop was most frequently found). The core area of the home range is represented by 50% MCP, with the total extent of the home range represented at 100% MCP. Range use, represented by the location of troop centroids at half hour intervals, and sleep sites for each troop are shown in Figures 3.6-3.8.

Table 3.5. Home range sizes for each troop in km^2 at 50%, 90% and 100% minimum convex polygons. Home ranges are provided for each time period.

Time Period	Troop	50% MCP	90% MCP	100% MCP
1	RBM	0.0892 km^2	0.3883 km^2	2.2239 km^2
	RST	0.0767 km^2	0.2653 km^2	1.4938 km^2
2	PT	0.0321 km^2	0.1855 km^2	1.2354 km^2
	RBM	0.0793 km^2	0.2881 km^2	1.7308 km^2
	RST	0.0704 km^2	0.2264 km^2	1.4362 km^2
3	PT	0.0343 km^2	0.1620 km^2	1.2856 km^2
	RBM	0.0551 km^2	0.2380 km^2	1.4675 km^2
	RST	0.0740 km^2	0.2151 km^2	1.1606 km^2

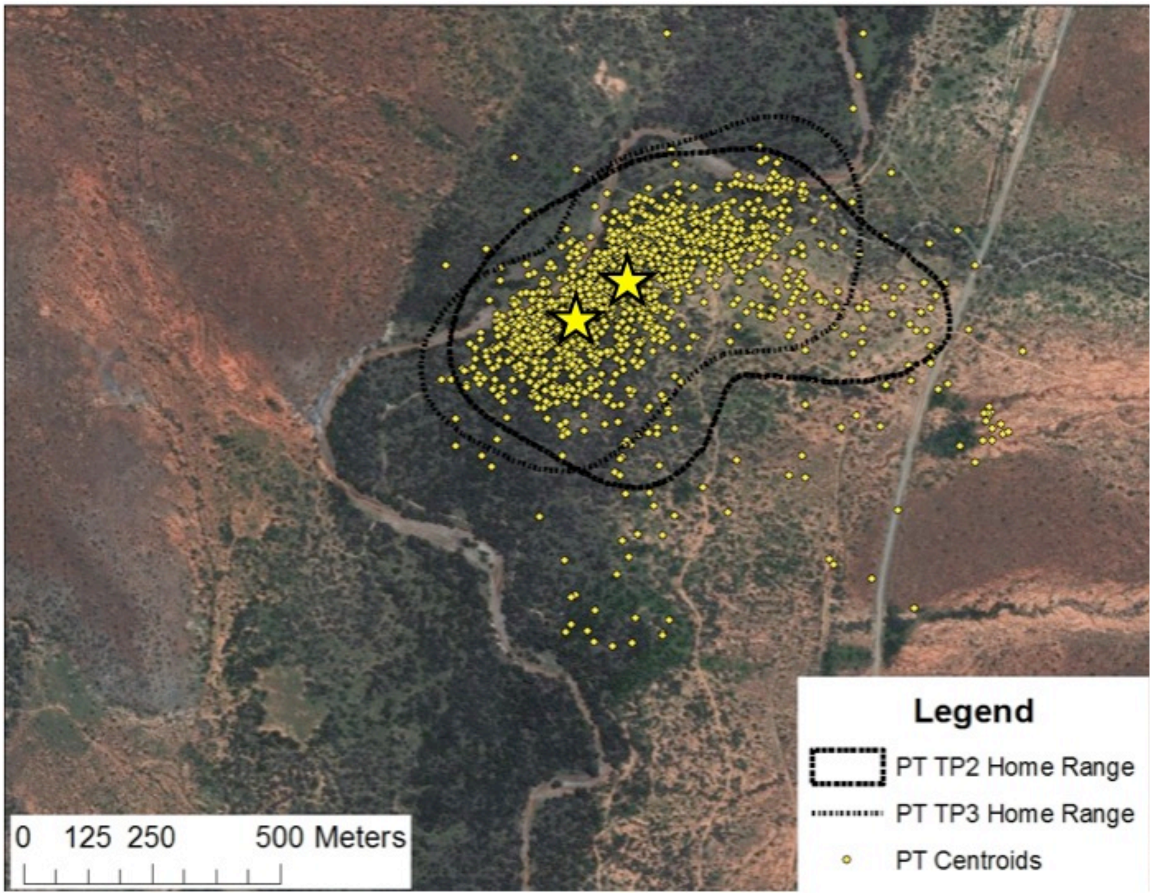

Figure 3.6. Map of the home ranges of PT in time period 2 and 3 (data are not available for PT in time period 1). The stars indicate PT sleep sites. Home ranges are represented at 95% minimum convex polygons. TP2 and TP3 in the legend refer to time period 1 and time period 2.

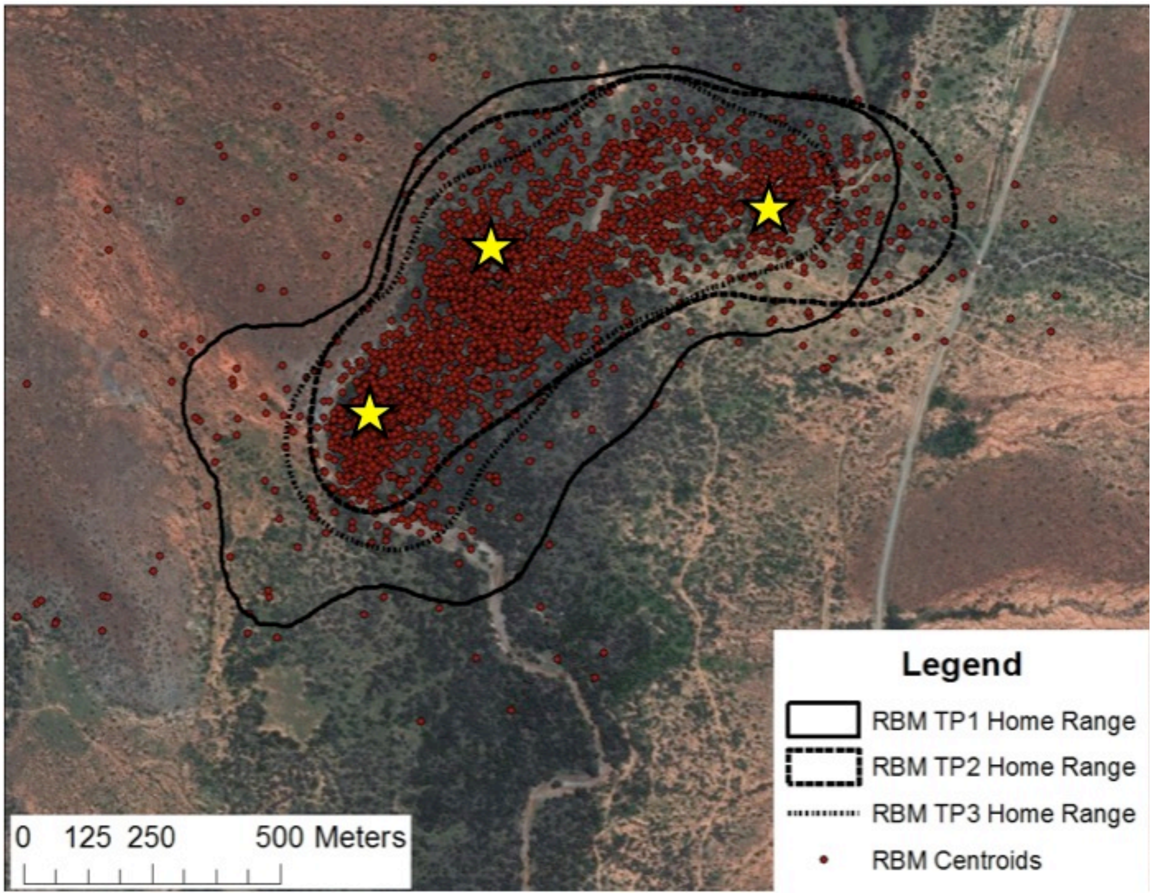

Figure 3.7. Map of the home ranges of RBM in time period 1, 2 and 3. The stars indicate RBM sleep sites. Home ranges are represented at 95% minimum convex polygons. TP1, TP2 and TP3 in the legend refer to time period 1, 2 and 3.

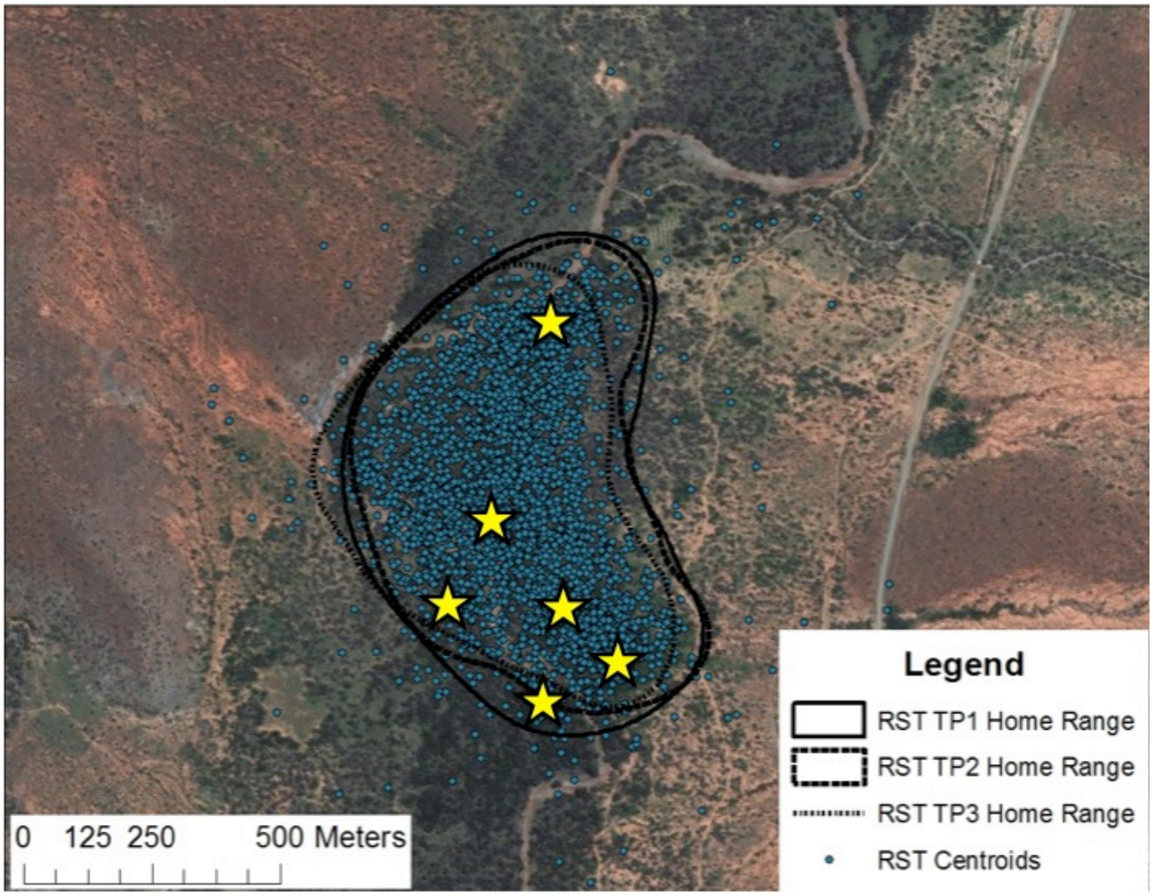

Figure 3.8. Map of the home ranges of RST in time period 1, 2 and 3. The stars indicate RST sleep sites. Home ranges are represented at 95% minimum convex polygons. TP1, TP2 and TP3 in the legend refer to time period 1, 2 and 3.

3.3 Areas of Overlap

3.3.1 Size of Overlap Areas

Home range overlaps for each troop were calculated for each of the three time periods, and the extent to which the 50% MCP and 100% MCP home range areas were affected is given in Table 3.9 and illustrated in Figures 3.11-3.13). Table

3.10 provides the percentage of each troop's core and total home range that overlapped with neighbouring troops.

Table 3.9. Areas of overlap in km^2 between each pair of troops (RBM – RST, PT – RBM, and PT – RST) at 50% and 100% minimum convex polygons.

Time Period	Overlapping Troops	50% MCP Overlap	100% MCP Overlap
1	RBM-RST	0.0096 km^2	0.9985 km^2
2	PT-RBM	0.0055 km^2	1.0826 km^2
	PT-RST	0.0036 km^2	0.9080 km^2
	RBM-RST	0.0025 km^2	1.0567 km^2
	RBM-RST-PT	0.0008 km^2	0.8025 km^2
3	PT-RBM	0.0034 km^2	0.8194 km^2
	PT-RST	0.0093 km^2	0.7875 km^2
	RBM-RST	0.0084 km^2	0.7145 km^2
	RBM-RST-PT	0.0027 km^2	0.5718 km^2

Table 3.10. Percentage of each troop’s home range core, at 50% minimum convex polygon (MCP), and total home range, at 100% MCP, that overlapped with neighbouring troops.

Time Period	Overlapping Troops	50% MCP Overlap	100% MCP Overlap
1	RBM	10.76 %	44.90 %
	RST	12.52 %	72.47 %
2	PT	25.86 %	96.17 %
	RBM	9.08 %	77.24 %
	RST	7.53 %	80.92 %
3	PT	29.15 %	77.78 %
	RBM	16.52 %	65.56%
	RST	20.27 %	80.15 %

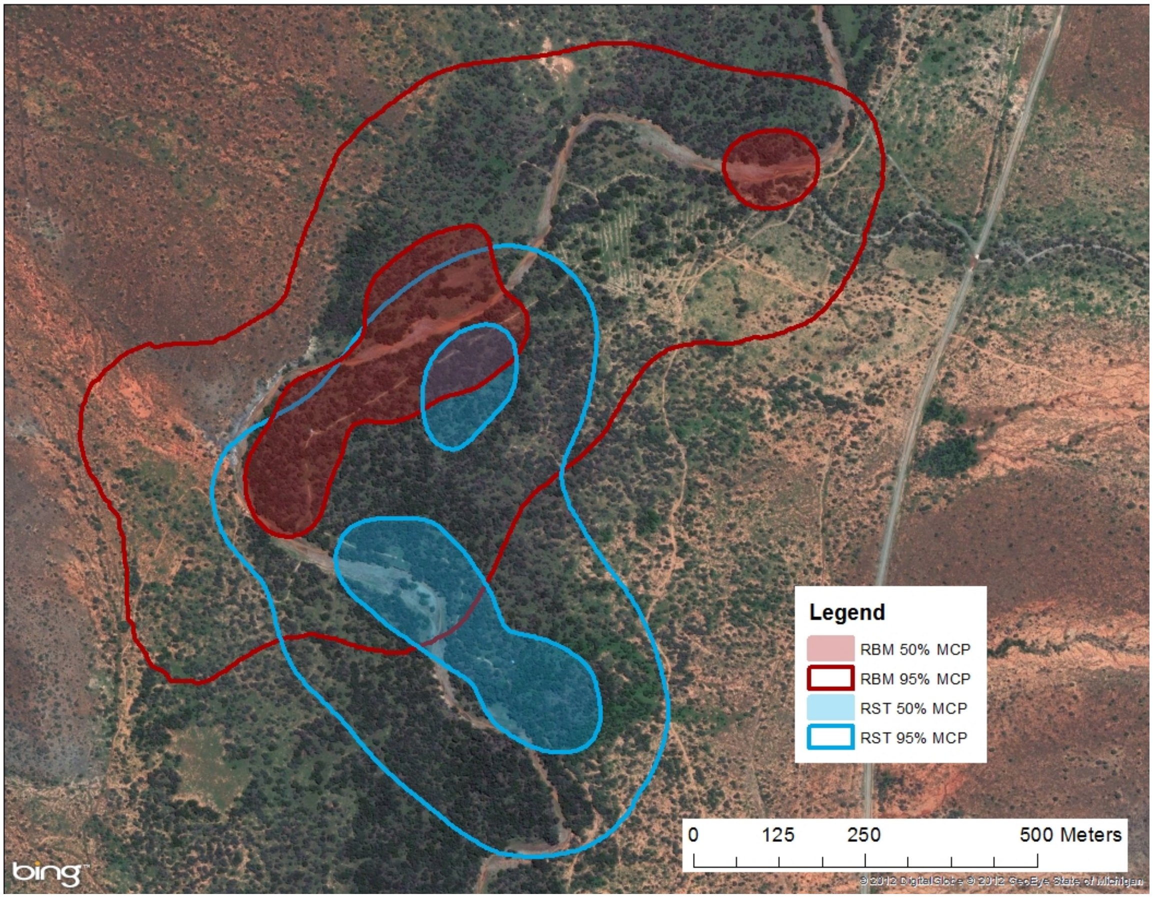

Figure 3.11. Map of the field site with the home ranges of RBM and RST outlined at 50% MCP (core) and 95% MCP (periphery) during the time period 1.

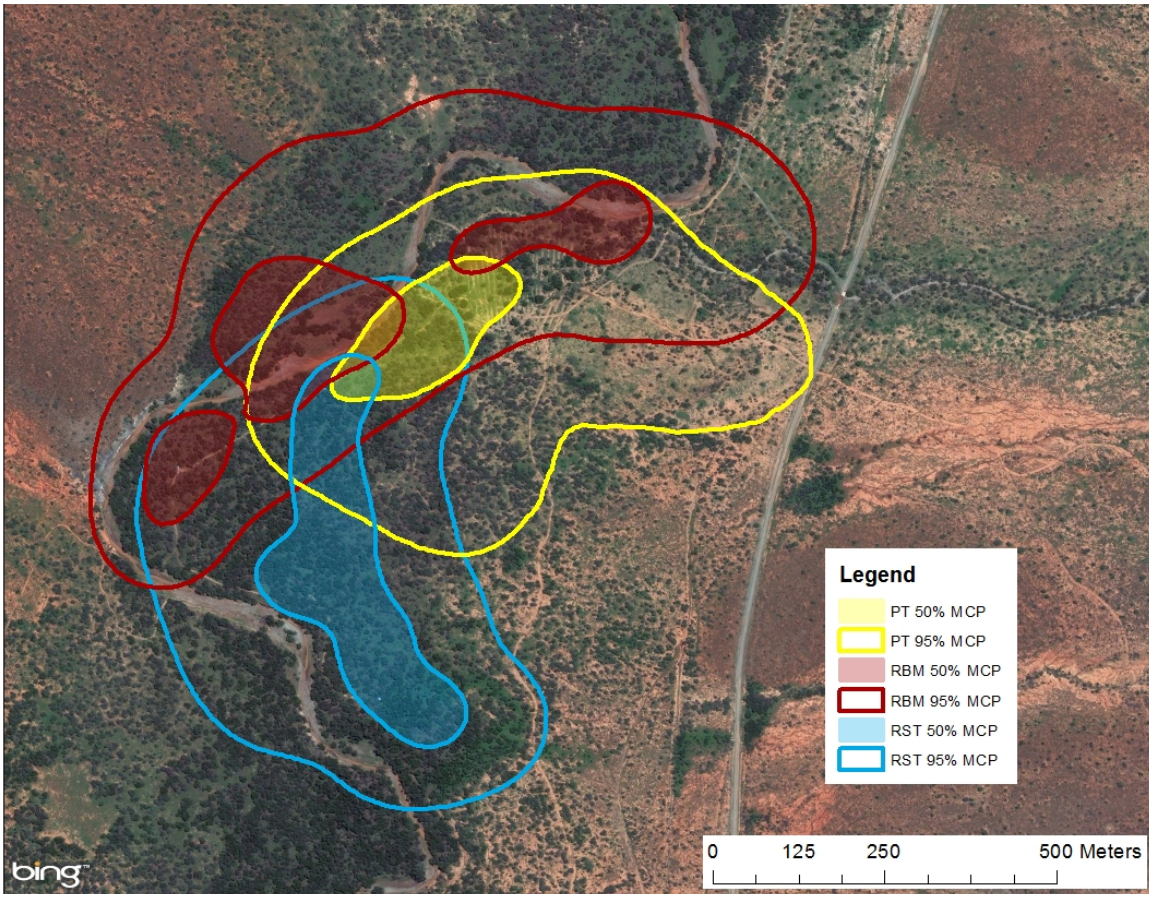

Figure 3.12. Map of the field site with the home ranges of RBM, RST and PT outlined at 50% MCP (core) and 95% MCP (periphery) during the time period 2.

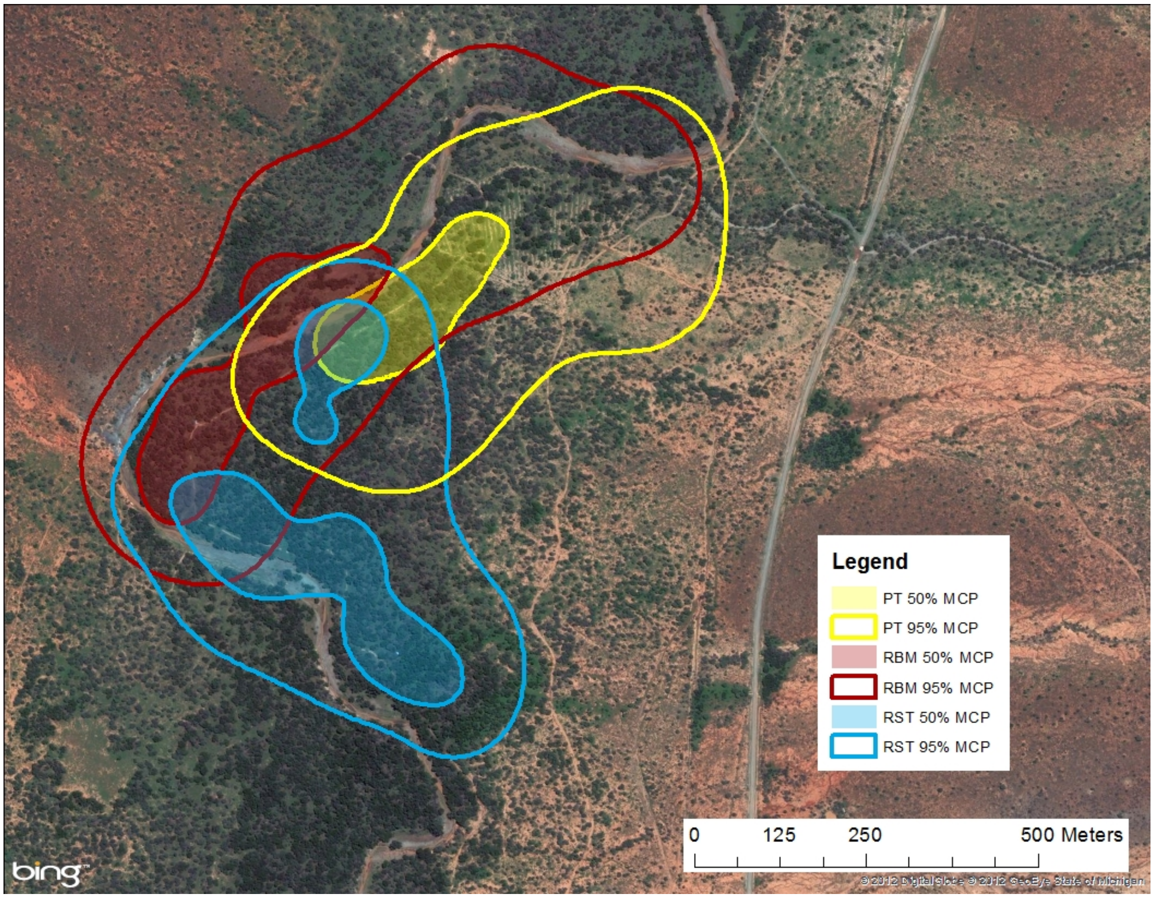

Figure 3.13. Map of the field site with the home ranges of RBM, RST and PT outlined at 50% MCP (core) and 95% MCP (periphery) during the time period 3.

3.3.2 Use of Overlap Areas

The home ranges of the three habituated troops overlapped extensively. In primate populations where home ranges overlap to this degree, groups spend less time in overlap zones compared to those areas they occupy exclusively. Figures 3.11-3.13 suggest that this may not be the case in this vervet population, as the core regions, or the regions that the troops occupy and exploit more frequently than peripheral areas, also overlap. To investigate the use of these overlap areas, I used the simple ratio index to determine the percentage of use of the various overlap areas by each habituated troop (Table 3.14). Unlike other studies (e.g Wrangham, Crofoot, Lundy, & Gilby, 2007), overlap areas were not extensively under-used (see Table 3.15 for use of exclusive space). A large proportion of centroid points were, in fact, recorded in 100% MCP overlap areas.

Table 3.14. Use of overlap areas by PT, RBM and RST across time period 1, 2 and 3. Use is defined as the number of GPS centroid points taken within the overlap area compared to the total number of GPS centroid points recorded. Percent values indicate the percentage of total GPS points that fall within the defined overlap area.

Time Period	Overlapping Troops	Troop	Total Number of GPS Points	Use of 50% MCP Overlap Area		Use of 100% MCP Overlap Area	
				GPS Points	%	GPS Points	%
1	RBM-RST	RBM	704	56	8%	566	80%
		RST	678	43	5%	669	99%
2	PT-RBM	PT	809	47	6%	803	99%
		RBM	1234	27	2%	1215	98%
	PT-RST	PT	809	33	4%	798	99%
		RST	1402	44	3%	1367	98%
	RBM-RST	RBM	1234	17	1%	1218	99%
		RST	1402	29	2%	1398	100%
	All	PT	809	2	0%	793	98%
		RBM	1234	3	0%	1203	97%
		RST	1402	7	0%	1365	97%

3	PT-RBM	PT	922	47	5%	896	97%
		RBM	1003	20	2%	963	96%
	PT-RST	PT	922	158	17%	899	98%
		RST	1085	99	9%	1061	99%
	RBM-RST	RBM	1003	88	9%	980	99%
		RST	1085	65	6%	897	83%
	All	PT	922	40	4%	882	96%
		RBM	1003	15	1%	952	95%
		RST	1085	22	2%	876	81%

Table 3.15. Use of exclusive space by PT, RBM and RST across time period 1, 2 and 3. Use is defined as the number of GPS centroid points taken within the exclusive area compared to the total number of GPS centroid points recorded. Percent values indicate the percentage of total GPS points that fall within the area of exclusive space.

Time Period	Troop	Total GPS Points	Use of Exclusive Space	
			GPS Points	%
1	RBM	704	138	33.81 %
	RST	678	9	1.33 %
2	PT	809	1	0.12 %
	RBM	1234	4	0.32 %
	RST	1402	2	0.14 %
3	PT	922	9	0.98 %
	RBM	1003	12	1.20 %
	RST	1085	3	0.28 %

3.4 Defendability Index

Mitani & Rodman (1979) argued that the ability of an animal or a group of animals to defend a territory depends on the animal or group's ability to monitor the boundaries of the given territory and to detect territory intrusion by conspecifics. Territorial species have an index value of greater then one. Whether a primate species defended a territory can be predicted by an index of defendability:

$$D = \frac{d}{\sqrt{(4A/\pi)}}$$

where D is the defendability index, d is the mean day journey length (km) and A is the area of the home range (km^2). Index of defendability values for each troop are given in Table 3.16. In all instances, index values are equal to or above one, indicating that troop home ranges are defendable. As the calculated day journey lengths are minimum estimates, the index values provided are underestimates of the actual defendability of the home ranges. The actual values of D, particularly in the summer months (time period 1 and 3), will be higher.

Table 3.16. Index of defendability values for each troop across each time period.

Troop	Time Period 1	Time Period 2	Time Period 3
PT	*No Data*	1.00	1.00
RBM	1.17	1.41	1.47
RST	1.40	1.22	1.15

3.5 Frequency of ITE Occurrence

Intertroop encounters (ITEs) have often been used as a measure of territorial behaviour (Harrison, 1983), and result from defence of resources from neighbouring conspecifics. To understand the expression of territoriality in this population more fully, I investigated the frequency of ITE occurrence in relation to mating season, seasonal shifts, areas of high foraging frequency, and differing areas of a troop's home range (core versus periphery). These various relationships were investigated in an effort to determine what the vervet groups may actively be competing over.

3.5.1 Raw Frequency of ITE Occurrence

The raw frequency of ITE occurrence, as well as the number of total days of observation on each habituated troop by time period is given in Table 3.17.

Table 3.17. Raw frequency of ITE occurrence and number of observation days with each troop, across the three time periods.

Time Period	Months	Troop						Total	
		PT		RBM		RST			
		Days	ITEs	Days	ITEs	Days	ITEs	Days	ITEs
1	Oct-Mar	*No Data*		52	41	47	112	99	153
2	Apr-Sep	85	16	83	112	89	82	257	210
3	Oct-Mar	51	34	51	73	60	28	162	135
Total		136	50	186	226	196	222	518	498

3.5.2 Frequency of ITE Occurrence by Person Hour

The ratio of ITEs per monthly person hours (total number of ITEs in a month, divided by the total number of person hours in a month), per study month was compared across troops and is shown in Figure 3.18. As observation hours differed for each troop, calculating ITE occurrence by person hour allowed for a more accurate comparison across troops. The frequency of ITE occurrence by person hour was used in all ITE analysis.

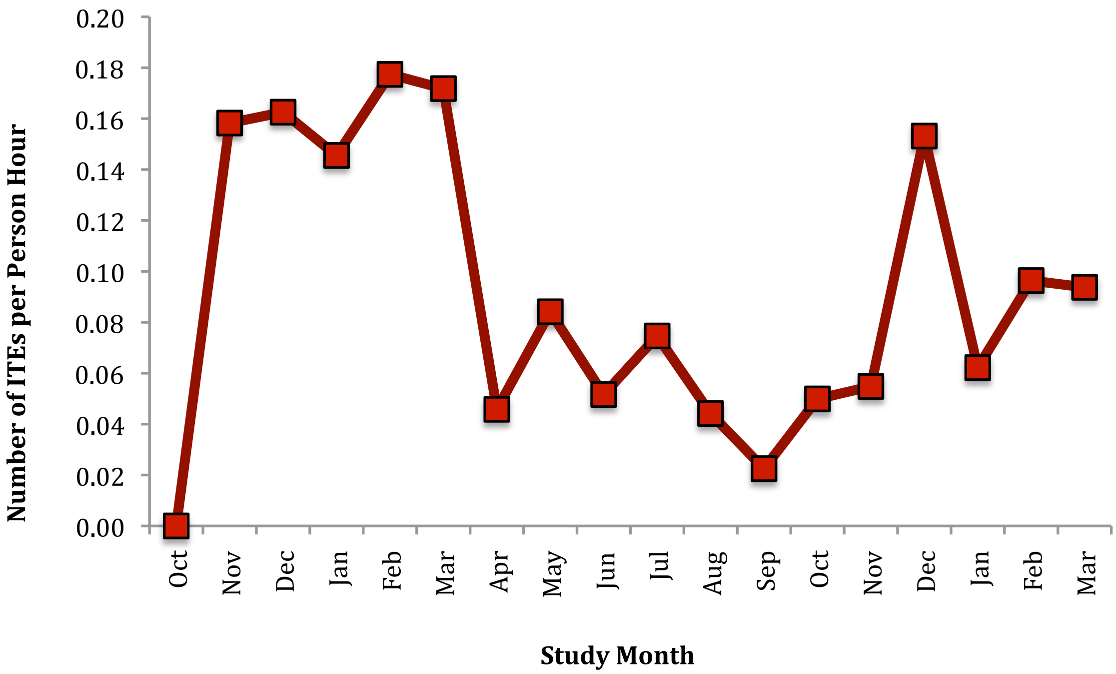

Figure 3.18. The ratio of ITEs per person hour/month by study month.

3.5.3 Frequency of ITE Occurrence in the Mating Season

If vervet monkeys were practicing mate defence, I predicted that the frequency of ITE occurrence would increase in the mating season, compared to the remaining study months. In order to test this prediction, the study months were divided into two categories: mating season months (March, April, May, June 2012, and March 2013) and remaining study months (Figure 3.19). A repeated measures *t* test was conducted to determine whether ITE frequency per person hour differed in the mating season (M = 0.34, SD = 1.95) compared to the remaining months (M = 0.19, SD = 1.12). The mean and standard deviation are given in ITEs per person hour. Both variables were log transformed, which improved skewness but did not eliminate it. There was no significant difference in the frequency of ITEs per person hour in the mating season compared to the remaining months; $t(190) = -1.172$, p = 0.242 (2-tailed).

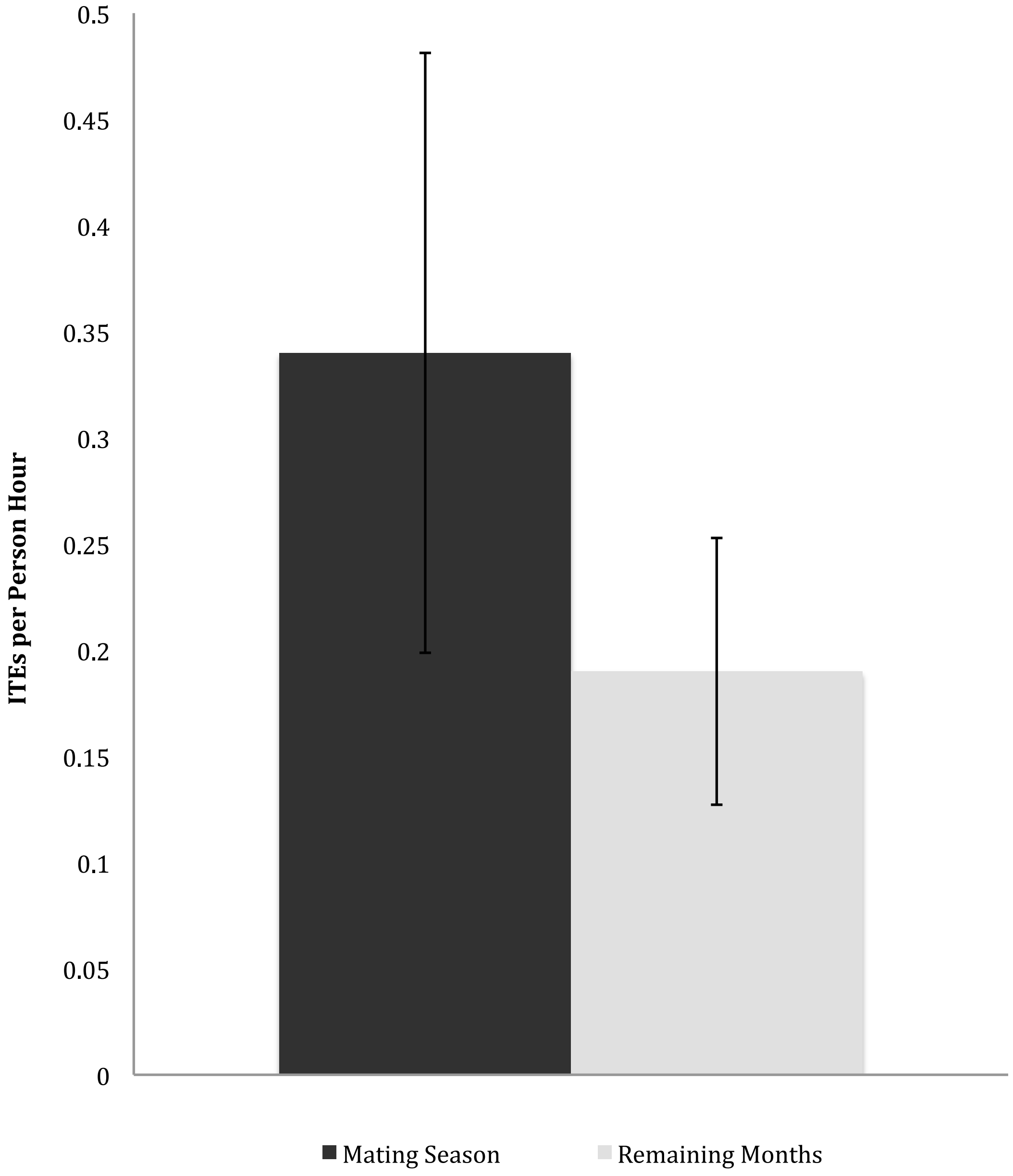

Figure 3.19. Frequency of ITE occurrence in the mating season (March, April, May, June 2012, and March 2013) compared to the remaining months of study. The vertical bars indicate standard error.

3.5.4 Frequency of ITE Occurrence Across Seasons/Time Periods

The frequencies of ITE occurrence across the rainy/summer season and the dry/winter were evaluated in an effort to determine if differences in the availability of resources across seasons resulted in a shift in the competition for resources. If intraspecific competition for resources increased in the winter months, when food resources should be less readily available, I predicted that ITE frequency would increase. Winter season is equivalent to time periods 2, and summer seasons are equivalent to time period 1 and 3.

As data were not available for PT in time period 1, two mixed-design ANOVA's were conducted. The first ANOVA compared all three habituated troops across time period 2 and 3, and the second ANOVA compared RBM and RST across all three time periods. The variables of ITEs/Person Hour across time period 1, 2 and 3 were all highly skewed but transformation did not improve skewness, and so the variables were left in their raw form. The mean and standard deviation of person hours per day on each troop, per time period, are given in Table 3.20. The mean numbers of ITEs per day and per person hour are also given.

Table 3.20. Mean and standard deviation of person hours per day, ITEs per day and ITEs per person hour across each troop, in each time period.

Troop	Time Period	Number of Days		Person Hours	ITEs/Day	ITEs/Person Hour
PT	2	*n* = 85	*M*	7.75	0.18	0.013
			SD	7.97	0.52	0.036
	3	*n* = 51	*M*	10.22	0.65	0.063
			SD	3.29	0.91	0.097
RBM	1	*n* = 52	*M*	10.21	0.77	0.065
			SD	6.23	1.77	0.127
	2	*n* = 83	*M*	13.25	1.30	0.606
			SD	9.61	1.99	2.81
	3	*n* = 50	*M*	10.25	1.18	0.735
			SD	4.43	1.32	2.704
RST	1	*n* = 47	*M*	9.39	1.96	0.400
			SD	7.00	2.83	1.189
	2	*n* = 89	*M*	12.86	0.92	0.111
			SD	9.04	1.67	0.438
	3	*n* = 53	*M*	11.11	0.47	0.036
			SD	4.52	0.72	0.053

The first mixed-design ANOVA, accounting for all three troops across time period 2 and 3, was conducted. As Mauchly's test for sphericity was significant, the

Geisser-Greenhouse correction is reported. Table 3.21 displays the main effects and interactions. While there was no significant effect of time, or of troop by time, there was a significant effect of troop. These results must be interpreted with caution, however, as Levene's test found significant variance in the time variables. The results of follow-up pairwise comparisons using Dunnett T3 post hoc tests revealed a significant difference in the frequency of ITE occurrence between PT and RBM (p = 0.037) and RBM and RST (p = 0.046), but found no significant difference between PT and RST (p = 0.134).

Table 3.21. Results of the mixed-design ANOVA comparing frequency of ITE occurrence across time period 2 and 3, across all troops.

Time	$F(1, 151) = 0.087$, $p = 0.768$	partial $n^2 = 0.001$
Troop	$F(2, 151) = 6.728$, $p = 0.002$	partial $n^2 = 0.082$
Time x Troop	$F(2, 151) = 0.134$, $p = 0.875$	partial $n^2 = 0.002$

A second mixed-design ANOVA, accounting for RST and RBM across all three time periods was conducted. As Mauchly's test for sphericity was significant, the Geisser-Greenhouse correction is reported. Table 3.20 displays the main effects and interactions. There is no significant effect of time, troop or time by troop. These results much also be interpreted with caution as Levene's test of equality of error variances was significant across all three time periods.

Table 3.22. Results of the mixed design ANOVA comparing RBM and RST across time periods 1, 2 and 3.

Time	$F(1.61, 153.08) = 0.501$, $p = 0.567$	partial $n^2 = 0.005$
Troop	$F(1, 95) = 3.380$, $p = 0.069$	partial $n^2 = 0.034$
Time x Troop	$F(1.61, 153.08) = 2.748$, $p = 0.079$	partial $n^2 = 0.028$

3.6 Location of ITE Occurrence

3.6.1 Foraging Density

3.6.1.1 Foraging Density Maps

Vervet troops in this study population may be competing for particular food patches, or specific areas rich in important food resources. Competition for resources may thus be more easily indicated by the spatial location of ITEs, and the observed frequency of foraging activity in those areas. To evaluate the value of an area in terms of foraging density, maps were created denoting areas of highest density of foraging activity. Using GPS coordinates and recorded activity of individuals on RBM and RST, recorded from October 2011 to August 2012, the location of all coordinates, where an individual was foraging, were plotted on a map. The kernel density tool in ArcGIS was then used to create surface maps, with areas of high foraging density indicated by the darker areas.

3.6.1.2 Location of ITEs in Relation to Foraging Density

The GPS coordinates of the ITEs that occurred with RBM (N = 141) and RST (N = 192) across the same time period (October 2011 to August 2012) were overlaid on each foraging density surface map (Figure 3.23 and 3.24). Each ITE coordinate was then matched with its associated raster cell value, or value of feeding density. One ITE from the focal troop RBM was deleted from the sample, as the ITE coordinates fell outside the range of the surface map and thus were given no foraging density value.

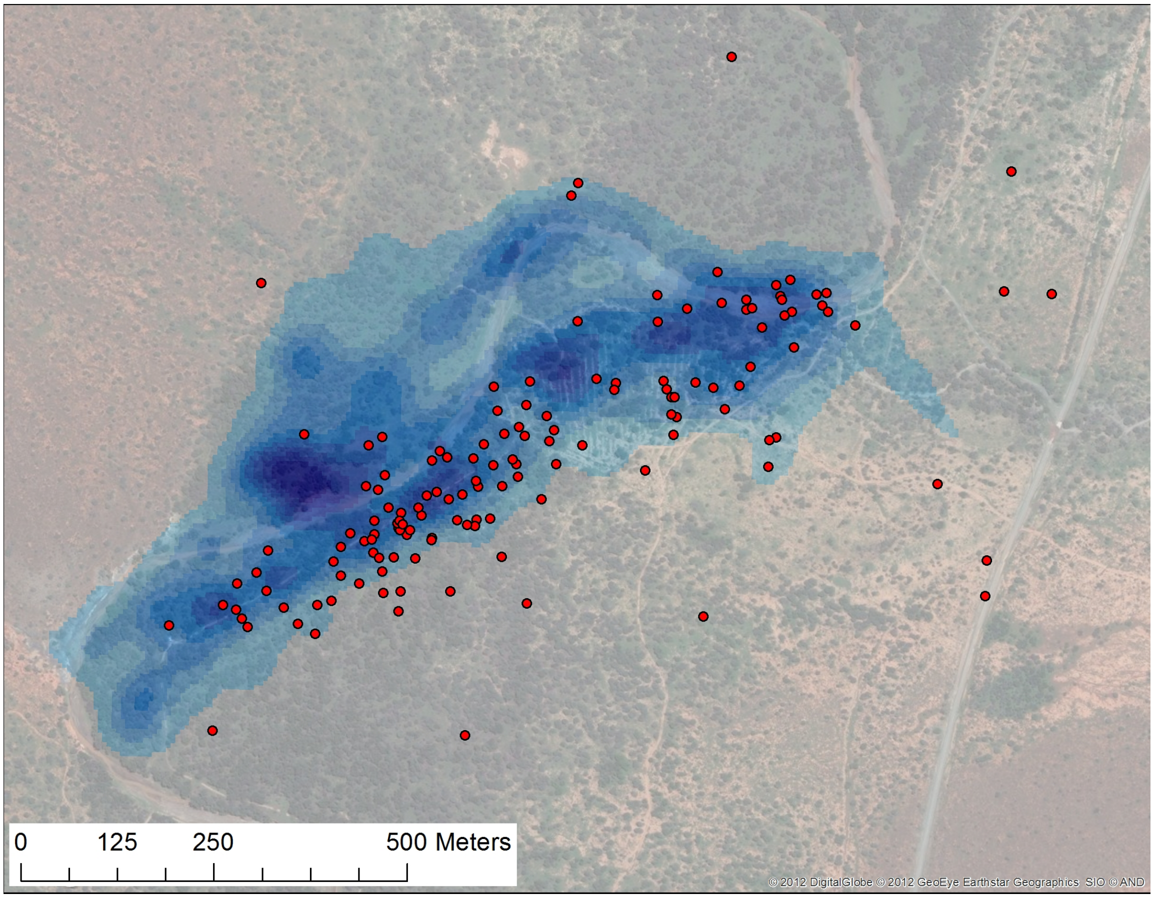

Figure 3.23. Surface map displaying the foraging density of RBM from October 2011 to August 2012. The location of all ITEs that occurred during the same period are overlaid (represented by the dark circles). The dark regions on the surface map represent the regions of high-density foraging activity.

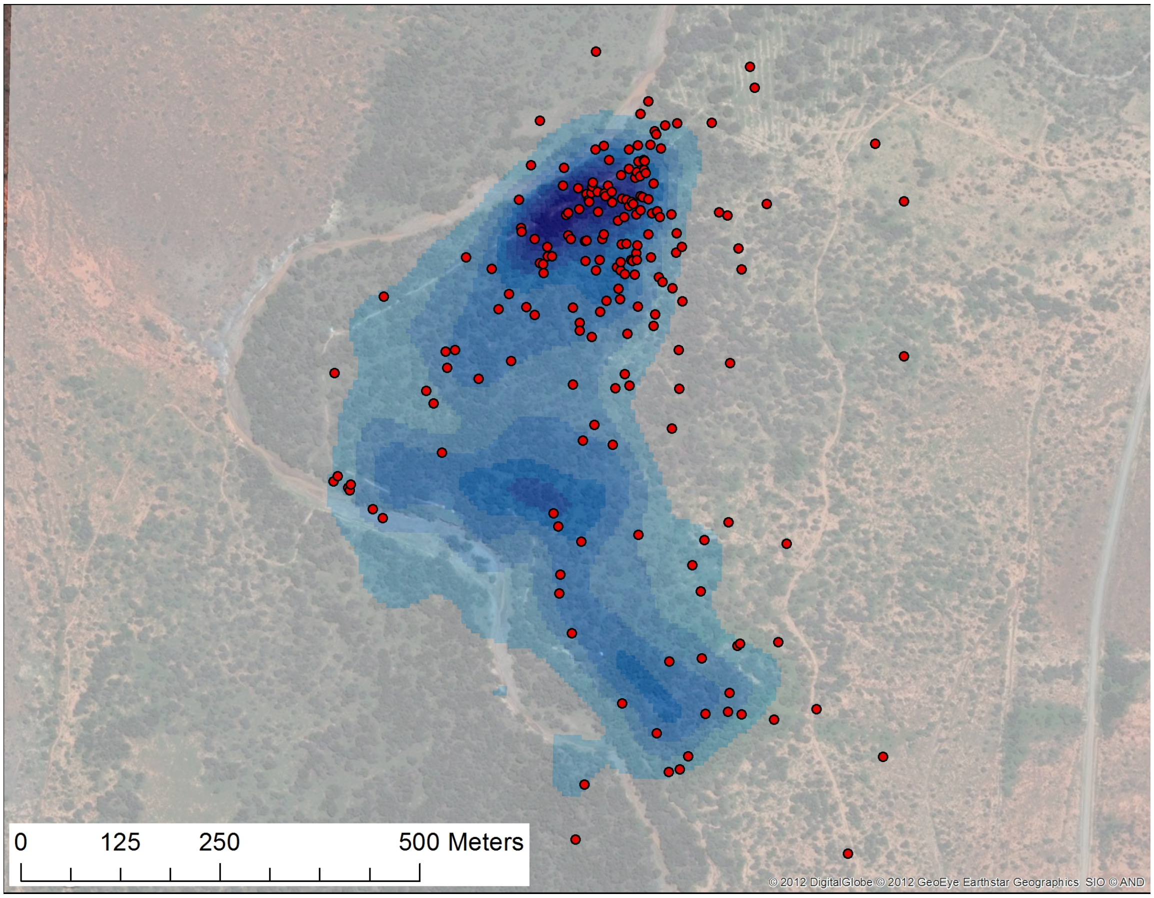

Figure 3.24. Surface map displaying the foraging density of RST from October 2011 to August 2012. The location of all ITEs that occurred during the same period are overlaid (represented by the dark circles). The dark regions on the surface map represent the regions of high-density foraging activity.

The mean and standard deviation of the feeding density value of the ITEs, derived from the kernel density surface map, are given in Table 3.25. Foraging density values were divided into 20% increments (1 = 0 – 19.9%, 2 = 20.0% – 39.9%, 3 = 40.0% – 59.9%, 4 = 60.0% – 79.9%, and 5 = 80.0% – 100.0%) (Figures 3.26 and 3.27). ITEs occurring in regions associated with the highest foraging density would fall under category 5, while the ITEs associated with the lowest foraging density would fall under category 1.

Table 3.25. Minimum, maximum, mean and standard deviation of kernel density values of the ITEs that occurred with RBM and RST.

Troop	*N* ITEs	Kernel Density Values of Foraging Density			
		Min	Max	*M*	*SD*
RBM	141	137.14	144 477.00	67 355.33	38 136.18
RST	192	616.36	265 924.00	108 204.50	74 947.49

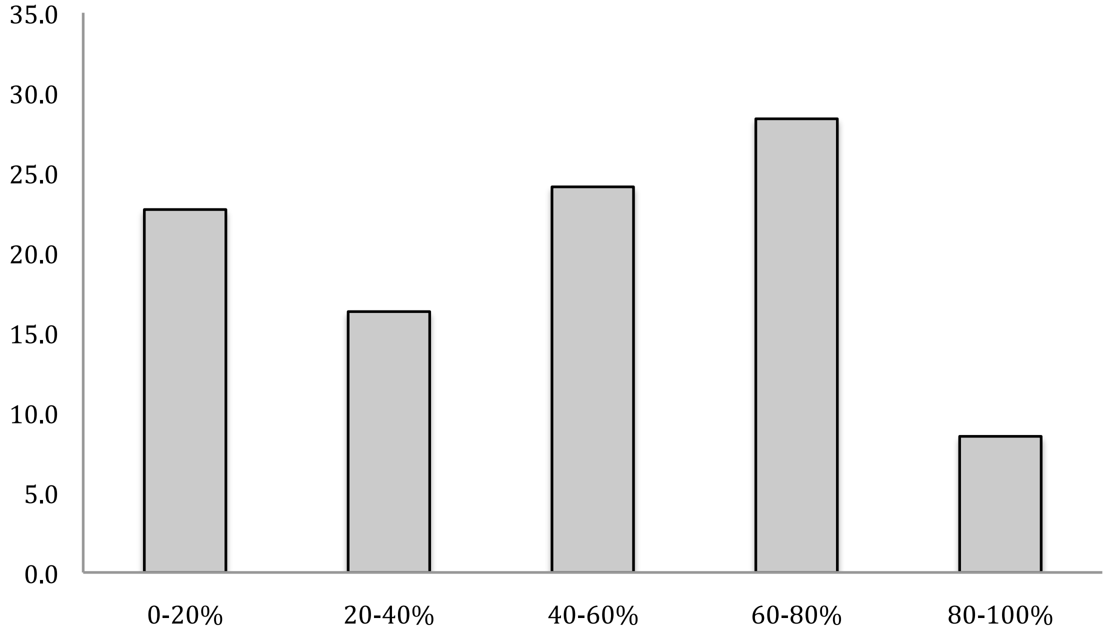

Figure 3.26. Percent of total ITEs with RBM that occurred in each category of foraging density.

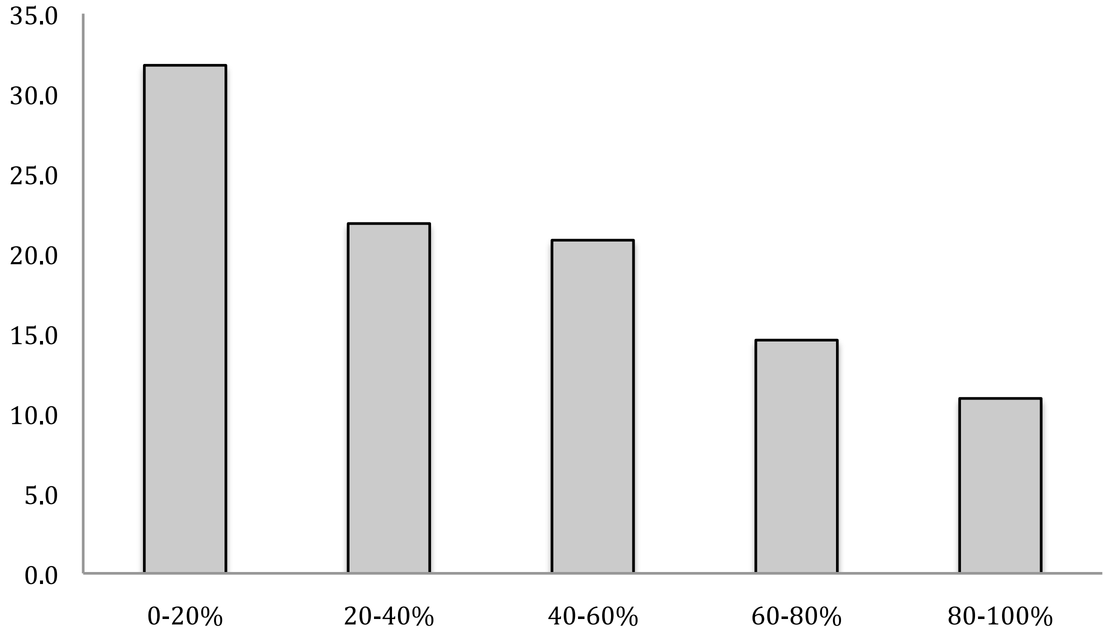

Figure 3.27. Percent of total ITEs with RST that occurred in each category of foraging density.

Chi^2 goodness of fit tests were used to compare the distribution of foraging densities associated with ITEs to the expected distribution. I predicted that the location of ITEs would not correspond to areas of high foraging density. I defined expected distribution as occurring evenly, meaning that ITEs were expected to be evenly distributed across areas of low and high foraging densities, and thus expected to occur in each of the previously defined categories (1 through 5) at equal rates. If the location of ITE occurrence does not correlate with areas of high density of foraging, as predicted, there should be no significant difference in the occurrence of ITEs across categories.

Contrary to prediction, there was a significant difference in the occurrence of ITEs across categories with RBM; $x^2(4, N = 141) = 16.908$, $p = 0.002$, and RST; $x^2(4, N$

= 192) = 24.406, $p < 0.001$. However, while the results contradict my prediction, they do not indicate an increased number of ITEs associated with higher foraging density values. The frequency of ITEs associated with each category of foraging density varies greatly with RBM, peaking in categories 3 and 4 (40-80%), but decreasing greatly in category 5 (80-100%). RST displays a much clearer pattern, with frequency of ITEs decreasing from category 1 through 5, indicating that ITEs occurred more frequently in areas of low foraging density.

3.6.2 Minimum Convex Polygons (MCPs)

Foraging density is likely to be higher in the core areas of home ranges, as these regions are more heavily exploited. If vervet troops are leaving preferred feeding areas, which are presumably closely associated with the core of the home range, to defend home range boundaries, we would expect ITE frequency to be higher in peripheral areas of the home range. The occurrences of ITEs by 10% home range MCP were therefore investigated. 10% MCPs were calculated using Home Range Tools for ArcGIS 9.3. The GPS coordinates for all ITEs were overlain on the MCP polygon maps to determine the number of ITEs that fell into each 10% MCP. Percent of total ITEs that occurred in each 10% MCP per time period, on each troop, are shown in Figures 3.28-3.30.

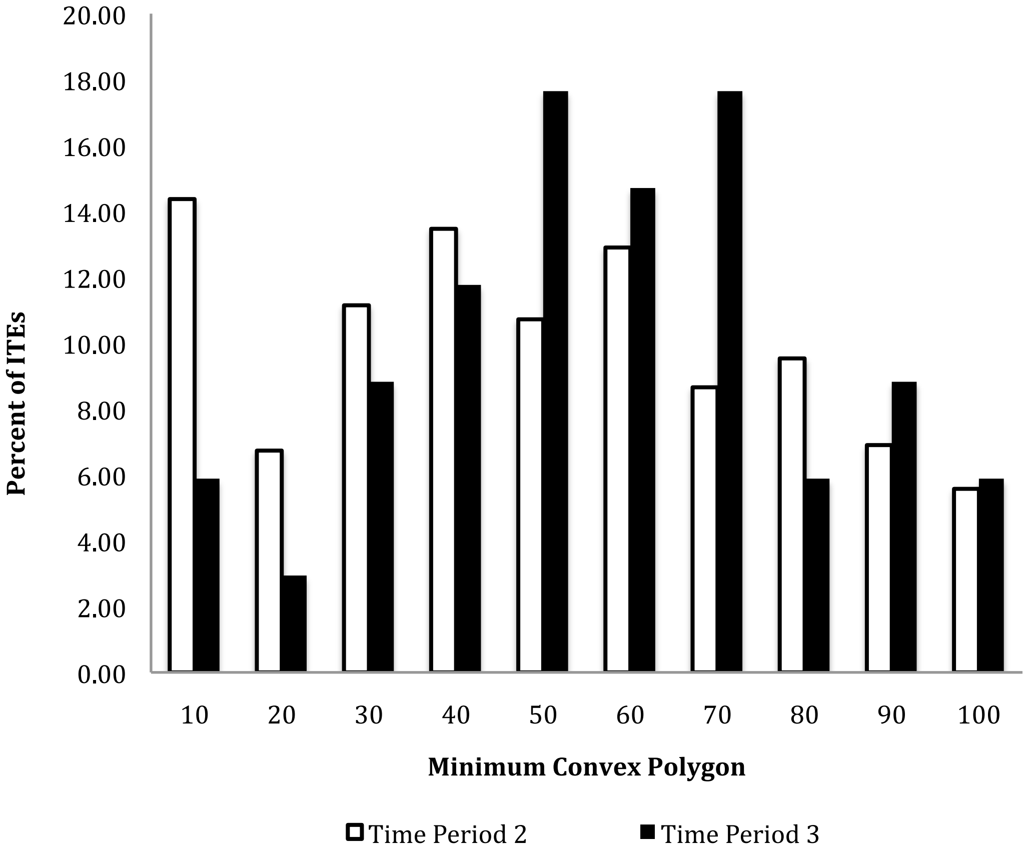

Figure 3.28. Percent of total ITEs per time period that occurred in each 10% MCP of PT's home range.

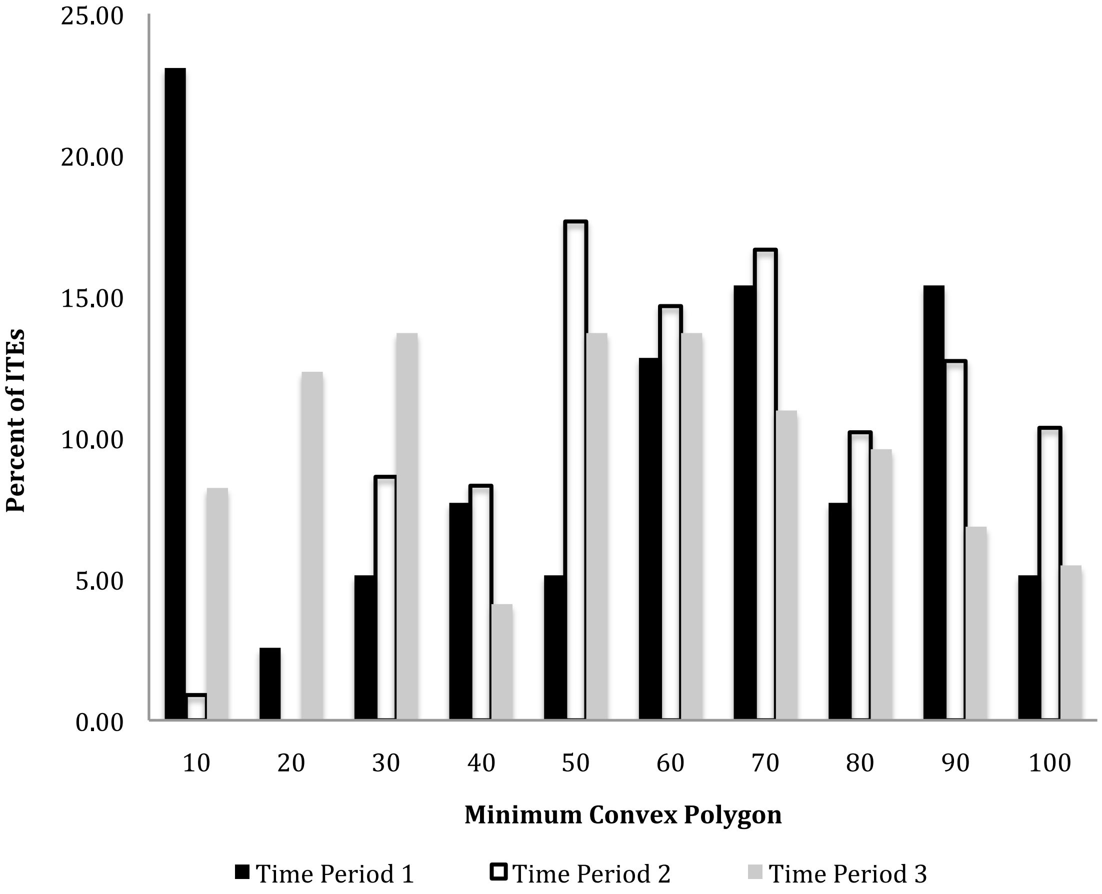

Figure 3.29. Percent of total ITEs per time period that occurred in each 10% MCP of RBM's home range.

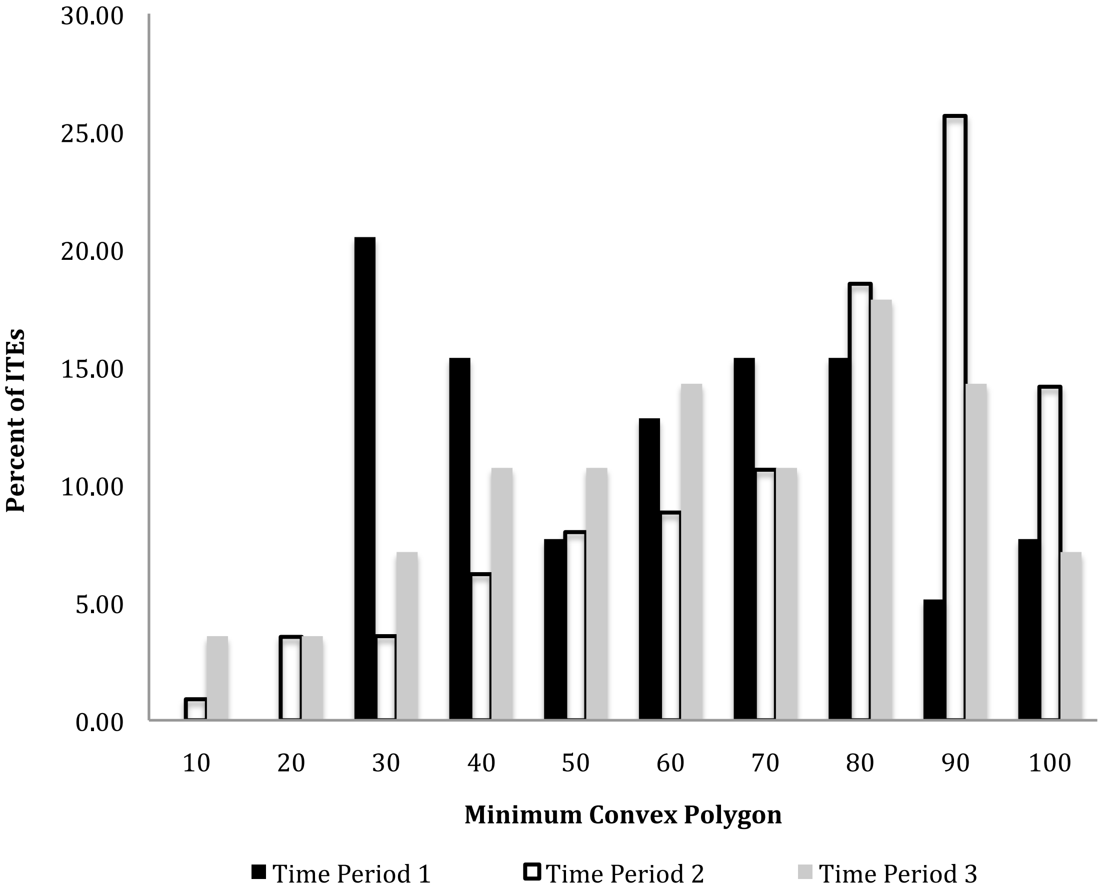

Figure 3.30. Percent of total ITEs per time period that occurred in each 10% MCP of RST's home range.

As can be seen in the figures above, there is no clear trend towards core defence, which would be indicated by a peak in ITE frequency in the 10-50% MCPs, nor is there a clear trend towards peripheral defence, which would be indicated by a peak in ITE frequency in the 50-100% MCPs. ITE frequency does increase slightly in the peripheral areas of the home ranges, particularly in the case of RST, where a clear increase in ITE frequency when moving towards the periphery is evidenced.

3.6.3 Conjoint Probability Index

ITE frequency may be slightly higher in peripheral areas of troop home ranges, as opposed to core regions, as troops may be actively seeking to defend home range boundaries. It is also possible, however, that ITEs are occurring in these peripheral regions simply because the odds of encountering neighbouring troops are higher in these peripheral regions. To further examine this possibility, ITEs were overlain on maps of polygons with calculated conjoint probability values.

In the map of overlain home ranges, separated into 10% MCP polygons, of two neighbouring troops, each polygon had an associated probability value describing the likelihood of encountering both troops simultaneously. The location of ITEs between the two troops was overlain on the appropriate overlapping map. Each ITE coordinate was then spatially matched with its associated conjoint probability index, to determine if ITEs do, in fact, occur in areas of higher probability of encounter. The mean and standard deviation of probabilities where ITEs occurred are given below (Table 3.31).

Table 3.31. The mean and standard deviation of conjoint probability values associated with the occurrence of ITEs across each pair of troops, in each time period.

Troop Pairs		Time Period 1	Time Period 2	Time Period 3
PT – RBM	*N*	*No Data*	68	47
	M		0.226	0.399
	SD		0.150	0.223
PT – RST	*N*	*No Data*	57	13
	M		0.211	0.233
	SD		0.129	0.233
RBM – RST	*N*	38	56	65
	M	0.336	0.193	0.263
	SD	0.238	0.138	0.180

A mixed-design ANOVA was conducted to determine if the probability values associated with the occurrence of ITEs differed significantly between pairs of troops, and whether they differed between time period 2 and time period 3. Two of the three difference scores were normally distributed, and so no variables were transformed. As Mauchly's test for sphericity was significant, the Geisser-Greenhouse correction is reported. Table 3.32 displays the main effects and interactions. Time, troop pairs and time by troop pairs were all significant.

Table 3.32. The results of the mixed design ANOVA comparing the conjoint probability values of ITEs between pairs of troops, and across time periods.

Time	$F(1, 115) = 119.843, p < 0.001$	partial $n^2 = 0.510$
Troop Pairs	$F(2, 115) = 4.866, p = 0.009$	partial $n^2 = 0.078$
Time x Troop Pairs	$F(2, 115) = 42.272, p < 0.001$	partial $n^2 = 0.424$

As previously mentioned, as PT was not under observation during the first time period, a repeated measures ANOVA was conducted to determine if there was a significant difference of probability scores with RBM and RST across the entire field study. As Mauchly's test for sphericity was significant, the Geisser-Greenhouse correction is reported. Time was highly significant; $F(2, 74) = 40.483$, $p < 0.001$, partial $n^2 = 0.522$, with a higher conjoint probability value of ITEs occurring in time period 1.

Lastly, Chi^2 goodness of fit tests were conducted to compare the frequency of conjoint probabilities associated with ITEs to the expected frequencies. If troops are not actively seeking out one another but simply encountering one another by chance, I predicted that ITEs will more frequently occur in regions of extensive overlap of highly used areas, where the probability of encountering neighbouring troops is high. If troops are actively seeking one another out, then the location of ITEs should not be significantly associated with areas of a high index of conjoint probability, though chance encounter will likely skew the results slightly towards areas of high conjoint probability. Conjoint probability values were categorized at 20% intervals

(1 = 0 – 0.19, 2 = 0.20 – 0.39, 3 = 0.40 – 0.59, 4 = 0.60 – 0.79, and 5 = 0.80 – 1.00). I defined expected frequency as occurring evenly, meaning that ITEs are expected to occur in each category at equal rates.

The results of the Chi^2 by time period, by troop, are given in Tables 3.33 – 3.35. In every instance, the null hypothesis was rejected, indicating that the categories did not occur equally. However, ITEs did not occur more frequently in areas of high conjoint probability value, where we would expect troops to more frequently encounter one another by chance, with ITEs instead occurring more frequently in areas of low conjoint probability (categories 1 and 2 most frequently).

Table 3.33. Chi^2 results comparing the frequency of ITE occurrence in each category of conjoint probability (score) to the expected frequency for RBM and RST across time period 1.

Troops	Score	Time Period 1		
		Frequency	Percent of ITEs	Statistics
RBM – RST	1	17	44.7 %	$x^2(4, N = 38) = 16.474$ $p = 0.002$ Scored $m = 2.29$
	2	7	18.4 %	
	3	6	15.8 %	
	4	2	5.3 %	
	5	6	15.8 %	

Table 3.34. Chi^2 results comparing the frequency of ITE occurrence in each category of conjoint probability (score) to the expected frequency for all pairs of troops across time period 2.

Troops	Score	Time Period 2		
		Frequency	Percent of ITEs	Statistics
PT – RBM	1	32	47.1 %	$x^2(4, N = 68) = 62.147$ $p < 0.001$ Scored $m = 1.69$
	2	25	36.8 %	
	3	11	16.2%	
	4	0	0 %	
	5	0	0 %	
PT – RST	1	25	43.9 %	$x^2(4, N = 57) = 60.281$ $p < 0.001$ Scored $m = 1.67$
	2	26	45.6 %	
	3	6	10.5 %	
	4	0	0 %	
	5	0	0 %	
RBM – RST	1	36	64.3 %	$x^2(4, N = 56) = 78.286$ $p < 0.001$ Scored $m = 1.50$
	2	12	21.4 %	
	3	8	14.3 %	
	4	0	0 %	
	5	0	0 %	

Table 3.35. Chi^2 results comparing the frequency of ITE occurrence in each category of conjoint probability (score) to the expected frequency for all pairs of troops across time period 3.

Troops	Score	Time Period 3		
		Frequency	Percent of ITEs	Statistics
PT – RBM	1	15	30.1 %	$x^2(4, N = 49) = 9.469$ $p = 0.050$ Scored $m = 2.47$
	2	10	20.4 %	
	3	14	28.6 %	
	4	6	12.2 %	
	5	4	8.2 %	
PT – RST	1	9	69.2 %	$x^2(4, N = 13) = 22.000$ $p < 0.001$ Scored $m = 1.69$
	2	0	0 %	
	3	3	23.1 %	
	4	1	7.7 %	
	5	0	0 %	
RBM – RST	1	29	44.6 %	$x^2(4, N = 65) = 42.000$ $p < 0.001$ Scored $m = 1.92$
	2	16	24.6 %	
	3	17	26.2 %	
	4	2	3.1 %	
	5	1	1.5 %	

3.7 Impact of ITEs on Troop Spatial Dynamics

3.7.1 Troop Spatial Deflection Post-ITE

Regions of high intraspecies density have been reported to mediate intraspecific conflict and competition by maintaining strong intertroop dominance hierarchies. Dominance hierarchies are generally determined by frequency of winning of ITEs. However, as the outcome was not often or easily determined in this population of vervets, intertroop dominance was investigated by examining the spatial deflection of a troop post-ITE. The deflection angles of troops post-ITE are also interesting in terms of their impact on the spatial patterns of the population as a whole.

To determine the angle of deflection following an ITE, the sample of observation days was restricted to days where at least one ITE took place between the two simultaneously observed troops. This left a total of 50 days where 202 ITEs occurred between one of three pairs of observed troops. Due to the reduced sample size, the sample was not split between time periods. Using a mixed-design ANOVA, deflection angles post-ITE were compared to angles of deflection from one troop centroid coordinate to another, and compared across troops (Figure 3.36). The mean and standard deviation of deflection angles before and after the occurrence of an ITE are given below (Table 3.37). As Mauchly's test for sphericity was significant, the Geisser-Greenhouse correction is reported. There was no significant effect of time, troop or time by troop (Table 3.38). Contrary to prediction, troop movement is not altered by the occurrence of an ITE.

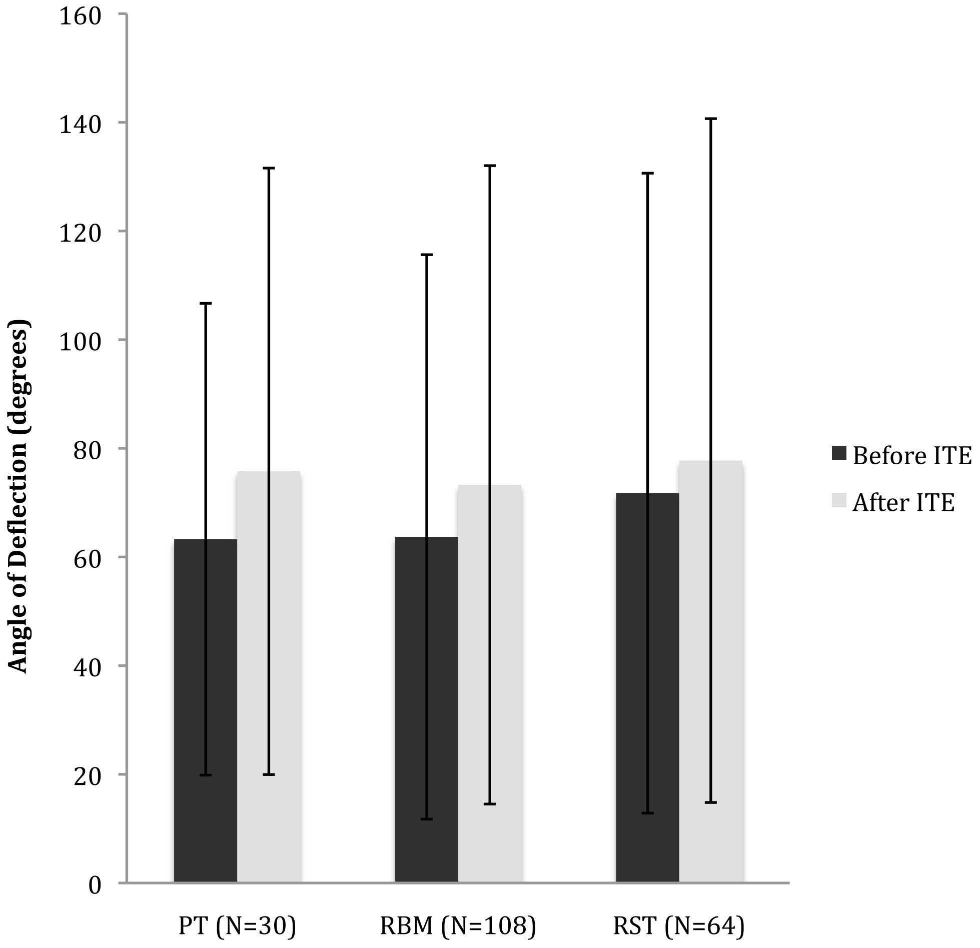

Figure 3.36. Angles of deflection before and after the occurrence of an ITE across PT, RBM and RST. The error bars represent standard deviation.

Table 3.37. Mean and standard deviation of angles of deflection before and after the occurrence of an ITE for each troop.

Troop	*n*	Before ITE		After ITE	
		m	*SD*	*m*	*SD*
PT	30	63.27	43.42	75.77	55.81
RBM	108	63.70	51.94	73.28	58.75
RST	64	71.75	58.89	77.75	62.93

Table 3.38. The results of the mixed design ANOVA comparing the angle of deflection before and after the occurrence of an ITE (time) and across troops.

Time	$F(1, 199) = 2.317$, $p = 0.130$	partial $n^2 = 0.012$
Troop	$F(2, 199) = 0.467$, $p = 0.628$	partial $n^2 = 0.005$
Time x Troop	$F(1, 199) = 0.084$, $p = 0.920$	partial $n^2 = 0.001$

3.7.2 Intratroop Spatial Cohesion Post-ITE

ITEs have no obvious impact on the spatial trajectory of a troop, but may have had an influence the spatial cohesion of a troop. To examine the influence of ITEs on troop spatial cohesion, troop spread was calculated at half-hour intervals, using GPS coordinates taken of individual troop members with RBM and RST, over the course of an observation day. Analysis was restricted to the days in which at least one ITE occurred with the focal troop when individual data was being collected.

The extent of spread between the two further individuals on a troop, at each half hour interval, was determined. The troop spread at the half-hour interval immediately proceeding the ITE was determined, as well as the troop spread at the half-hour interval immediately following the ITE (Figure 3.39).

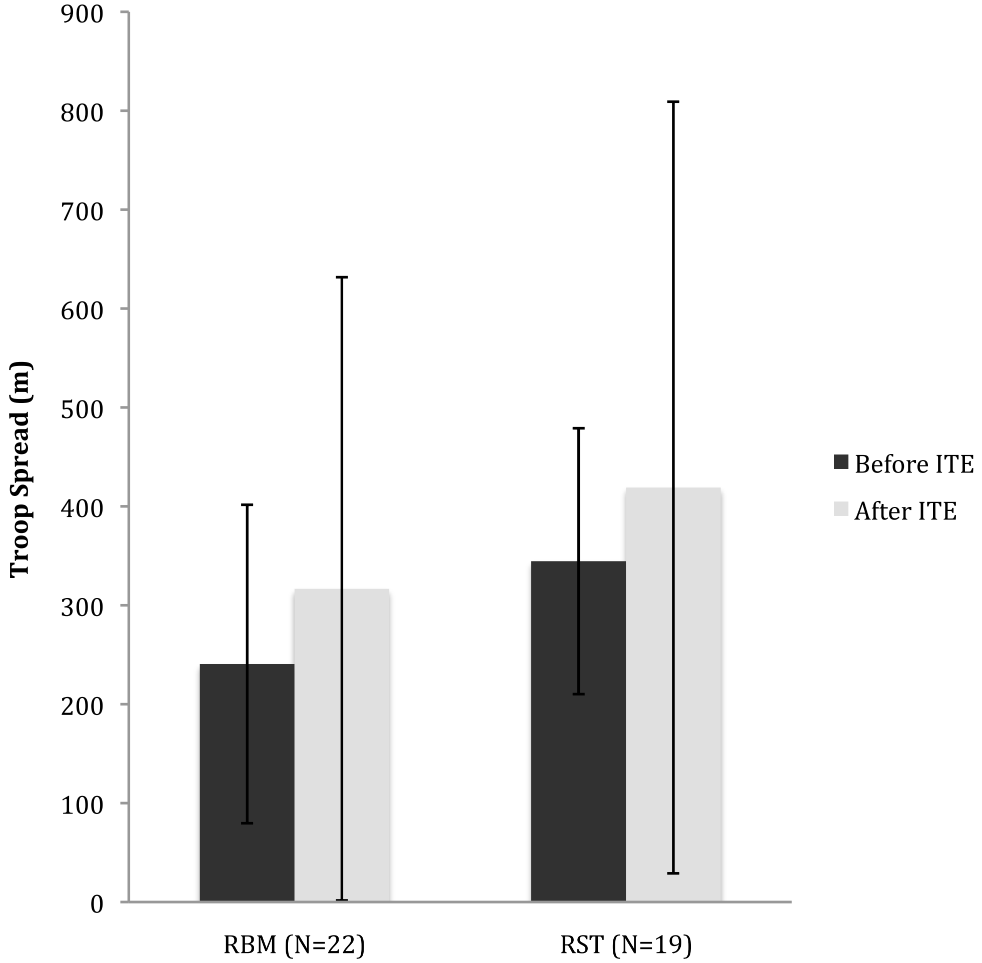

Figure 3.39. Troop spread in meters before and after the occurrence of ITEs across RBM and RST. The error bars represent standard deviation.

The mean and standard deviation of troop spread in meters before and after the occurrence of an ITE are given below (Table 3.40). Both before ITE and after ITE variables were highly skewed and log transformed. A mixed-design ANOVA was used to test whether there was a difference of troop spread before and after an ITE, and whether or not there was a difference between troops. The variables before and after ITE were entered as within-group factors, and troop was entered as the between-group factor. As Mauchly's test for sphericity was significant, the Geisser-Greenhouse correction is reported. There was no significant effect of time, troop or time by troop (Table 3.41).

Table 3.40. The mean and standard deviation of troop spread in meters before and after the occurrence of an ITE with RBM and RST.

Troop	*n*	Before ITE		After ITE	
		m	*SD*	*m*	*SD*
RBM	22	240.64m	160.988m	316.64m	315.044m
RST	19	344.58m	134.408m	419.05m	390.065m

Table 3.41. The results of the mixed-design ANOVA comparing troop spread across RBM and RST, and comparing troop spread before and after the occurrence of an ITE.

Time	$F(1, 39) = 0.538$, $p = 0.468$	partial $n^2 = 0.014$
Troop	$F(1, 39) = 2.838$, $p = 0.100$	partial $n^2 = 0.068$
Time x Troop	$F(1, 39) = 0.056$, $p = 0.331$	partial $n^2 = 0.024$

Chapter 4: Discussion

Several species within the *Clorocebus* genus have been described as exhibiting facultative territoriality. Despite this obvious and extensive variation in territorial expression across the genus, vervet monkeys, as a species, are repeatedly described as being highly territorial. The population of vervets described in this thesis, however, did not display the same behavioural characteristics evident in other vervet study populations, exhibiting large group sizes, high population density and extensively overlapping home ranges.

4.1 Population Spatial Dynamics

Day journey lengths in this population of vervet monkeys ranged from an average of 1260 m (PT in time period 2) to 2090 m (RBM in time period 2). There was a significant difference in the day journey lengths across troops and time period in time period 2 and 3. Day journey lengths for RBM and RST were significantly larger during time period 2, the winter season. Troops may have had to travel further to meet their dietary needs during this period.

The data confirm that home range sizes have not changed significantly from 2011, when they were calculated at 1.760 km^2 for RBM, and 0.637 km^2 for RST at 99 % minimum convex polygon (MCP) (Pasternak et al., 2012). In 2008, RBM and RST were reported to have exploited and defended much small areas of approximately 0.250 km^2 (McDougall, Forshaw, Barrett, & Henzi, 2010). A drought, however, in early 2009 forced the study troops to travel for access to water and thus greatly expand their home ranges (McDougall et al., 2010).

Across this 18-month study, RBM's home range size decreased substantially from time period 1 to time period 2, and decreased again slightly from time period 2 to time period 3. This may have been due the abundance of available food resources and water at the field site, reducing the need for the troops to travel further distances in search of food or water. RBM's core areas of use (represented by 50 % MCP) deceased slightly, and shifted substantially; encompassing two separate areas in time period 1, followed by three smaller areas in time period 2 and one large core area in time period 3. RST home range size remained relatively consistent across all three time periods. The core area or RST encompassed a fairly consistent area, but did shift from two separate areas in time period 1, to a smaller single area in time period 2, back to two separate areas in time period 3. The size of PT's core area and total home range remained relatively consistent across time period 2 and 3, but the total home range did shift considerably (there were no available data for PT in time period 1). RBM and RST followed similar patterns in decrease in home range size from time period 1 (summer) to time period 2 (winter), with a substantial decrease in RBM's home range size. These results are particularly interesting, given that day journey lengths in this period increased significantly for RBM and RST, indicating that the troops traveled further in a given day, but exploited a smaller region than in the previous time period.

RBM lacked neighbouring troops on the northwest and northeast boundaries of its home range. The lack of neighbouring troops in these areas allowed RBM to exploit these regions without the threat of intergroup competition or aggression. Vegetation density in these peripheral areas was noticeably less than those riparian areas along the river, suggesting that a scarcity of vegetation within the core of RBM's home range may have encouraged the exploitation of resources outside the usual home range boundary, and further from the core areas. Steady rainfall and consistent availability of food resources throughout the study period confirmed that conditions during this eighteen month period were favourable and resources abundantly available (unpublished data). The abundance of available resources may have led to a decrease in interspecific and intraspecific competition for resources during this field study. The costs of defending a large home range would therefore no longer be offset by the extensive benefits of resource access, and the decrease in RBM's home range size after time period 1 may have been a consequence of this.

In contrast to RBM, RST was completely surrounded by neighbouring troops, and thus expansion of home range size in response to limited resources, or any other intertroop or intratroop competitive factor, may not have been an option. The slight fluctuations in the home range of RST may instead follow seasonal fluctuations in the availability of resources, though more detailed data are required to confirm this. While the size of home range of PT actually increased slightly from time period 2 to time period 3, PT shows a pattern of spatial use similar to that of RBM. PT lacked neighbouring troops on the eastern and southeastern boundary of its home range. This may have allowed PT, in time period 2, to exploit these areas not occupied or shared with neighbouring troops, specifically expanding from the core area of its home range to the southeast; a region of low vegetation density.

While the size of PT's home range increased very slightly from time period 2 to time period 3, it also shifted to encompass areas of greater vegetation density along the river. As the shift from time period 2 to time period 3 is equivalent to the shift from the dry/winter months to the rainy/summer months, it is possible that a slight increase in the availability of resources in the summer months lead to a decrease in the need for PT to travel an extensive distance in a day, or to exploit areas of lower flora density.

Fluctuations in home range sizes and extent did not appear to favour any one troop, and there is no clear indication of any one troop substantially expanding its home range size and in turn, decreasing the size of the home range of a neighbouring troop. This lack of expansion and contraction in favour of or at the cost of a troop may be due to the extensive overlap of home ranges and the extensive use of these overlap areas. Overlap between troop home ranges extended from 44.90 % to 96.17 % of total home range area (at 100 % MCP), thus encompassing a huge portion of each troop's home range. Not only were these overlap zones large, they were also extensively exploited, with 80 – 99 % of all GPS centroids recorded within an area where two troop home ranges overlapped. Also of interest, a portion of the core areas of each troop's home range overlapped in each time period.

In primate groups inhabiting densely occupied areas, or those regions with high home range overlap, rarely do core regions of habitat overlap. Contrary to my prediction, and unlike many other primate species (e.g. Wrangham, Crofoot, Lundy, & Gilby, 2007), the study troops spent more time in areas of overlap than in areas of exclusive use. The extensive time spent in these areas, however, may simply be due to the large overlap of home ranges, the rarity of exclusive space, and high primate density. The core regions across all three study troops largely lie along the river, and clearly encompass the areas of more dense vegetation than peripheral areas. Perhaps this abundance of vegetation, and food resources, prevented the need for extensive intergroup competition, allowing the troops to exploit regions simultaneously. A second possibility is that the cost of foraging in less desirable but exclusive space is greater than the cost of exploiting shared areas; and thus overlap areas are used extensively. A third possibility is that the overlap areas are so extensive, that despite the shared space, the chance of encountering a neighbouring troop is very low. A fourth possibility is that the troops do not, in fact, exploit these areas concurrently but that the spatial data presented are simply not at a small enough temporal scale to reveal this.

This use of shared space may also stem from the inability of the study troops to successfully monitor and defend home range boundaries, and expel intruding conspecifics. The home ranges of all three troops were defendable (as indexed by D), with values ranging from 1.00 (PT, time period 2 and 3) to 1.47 (RBM, time period 3). PT's index value remained the same across time period 2 and 3; reflecting the lack of significant change in PT's home range size. RBM's index value increased from time period 1 to 3, as RBM's home range continuously decreased in size. Contrarily, the index values for RST decreased from time period 1 to 3, despite a slight decrease in home range size. The study troops could, therefore, successfully monitor and defend their home ranges throughout the 18-month study, according to Mitani and Rodman's defendability index (1979).

The slight fluctuations in home range size, day journey length and home range defendability may represent the continual intertroop negotiation of space in a highly dense, saturated population. These fluctuations may be much apparent or more easily associated with seasonal or behavioural shifts if investigated at a smaller temporal scale.

4.2 Intertroop Encounters

The frequency and the intensity of intertroop encounters (ITEs) are often used as measurements for the degree of territoriality, or level of competition, expressed in a species or a population of a species. ITEs were documented in the study population across the entire 18-month study period. Various predictions were made in an attempt to determine the type(s) of resource defence practiced by this population of vervets; specifically investigating whether vervets were competing for mates, access to particular food rich areas or access to all resources within their home ranges. If vervet monkeys were participating in mate defence, I hypothesized that the frequency of ITE occurrence would increase in the mating season, as compared to the remaining study months. There was no significant difference between the frequency of occurrence of ITEs per person hour between the mating season and all other remaining months. The vervet monkeys in this population do not, therefore, appear to be actively defending mates. Observers have also reported that males, who are generally active participants in mate defence in many primate species, rarely participated in ITEs, though further data are required to fully substantiate this claim.

If seasonal shifts in temperature and precipitation between the rainy/summer season (time period 1 and 3) and the dry/winter (time period 2) resulted in differences in the availability of resources, we would expect a shift in competition for resources; with higher intraspecific competition occurring in the winter. This increased competition should be evident by an increase in the number of ITEs occurring in the winter months (time period 2). When comparing frequency of ITES per person hour, there was no significant interaction of troops by season/time period, or a significant difference between seasons/time periods on a single troop or between troops. This suggests that competition did not substantially increase for food resources, or any other resource, seasonally, or from one time period to the next. However, this suggestion must be taken with caution as the temporal scale of ITE comparison, being by 6 month time period, may not be fine enough to accurately mirror minute seasonal shifts. The characteristics of resources are likely much more complicated than we understand or than I was able to show, with slight shifts in resource availability and quality occurring daily, weekly and monthly (Waser & Homewood, 1979).

If the vervet troops were not competing for seasonal resources, they may have been doing so for particular food patches, or important areas rich in food resources. If competition for specific food patches was taking place, the location of ITEs should be highly correlated to areas of high foraging density. As this population of vervets relies heavily on acacia trees, which are evenly and abundantly distributed across the field site, I hypothesized that no correlation would exist between ITE occurrences and areas of high foraging density. Contrary to prediction, there was a significant difference in the occurrence of ITEs across categories of foraging density. However, ITEs occurred more frequently in areas of low foraging density with RST, and in areas of medium foraging density (40-80 % foraging density values) with RBM. ITEs did not, therefore, occur more frequently in regions of high foraging density.

Butynski (1990) stated that resources should be both limited and defendable for territoriality to be expressed. In our study population, resources appear to be evenly distributed and abundantly available, as it suggested by the kernel density maps. Despite the availability of resources, the vervets clearly display some degree of territoriality, as is evidenced by the frequent occurrence of ITEs. The study troops may be defending entire regions of particularly important or variable resources through home range defence. Much like this study population, the *Colobus guereza* participates in aggressive ITEs with neighbouring groups, but does not use high-quality food patches (Wrangham, 1980). Territoriality in *C. guereza* has been explained as a means to minimize location costs by confining foraging to a small area with a consistent food supply (Wrangham, 1980). Kavanagh (1981) stated that the reliability of particular locations to produce food will favour spatial defence. Perhaps the study troops are not defending particular food patches, but defending access to all resources within the boundary of their home range through home range defence.

This led me to ask whether ITEs occurred more frequently in peripheral areas, where the foraging effort is likely to be lower than the core of the troop's home ranges and where home range boundary defence would take place? I examined the location of ITEs in terms of occurring in each 10 % MCP of each troop's home range, where the innermost core is represented by 10 % MCP, and the outermost periphery of the home range represented by 100 % MCP. I hypothesized that if the study vervets were displaying low levels of territorial behaviour, troops would avoid confronting neighbours and preferentially defend core areas (10 – 50 % MCP) of the home range when under pressure from conspecifics (instead of patrolling boundaries and encountering troops in peripheral regions). These core areas, where troops spend a majority of their time, were most heavily exploited and thus presumably contained the most valued resources. If, on the other hand, vervets were neither competing for mates or specific resources, they may have been competing with neighbouring troops for access to all resources within their home ranges.If the study troops were competing for space, I hypothesized that ITEs will occur more frequently on the periphery of troop home ranges (50 – 100 % MCP) than in the core areas.

The results suggest no clear trends towards either core (10 – 50 % MCP) or peripheral (60 – 100 % MCP) defence, with ITEs occurring across all MCPs, in each time time period. A slightly higher total number of ITEs did occur in the peripheral areas of the troop's home ranges, suggesting that the study troops may be competing against neighbouring troops for space along their home range boundary. However, this slight increase in the total number of ITEs in peripheral areas may simply be the result of a higher probability of encountering neighbouring troops in these peripheral, highly overlapping areas of the home ranges.

Given these data, I predicted that ITEs would occur more frequently where the probability of encountering neighbouring troops, and thus the conjoint probability values, was high. Contrary to my prediction, ITEs did not occur in regions of high probability of encounter more than in those regions of low probability of encounter. Across all pairs of troops in all time periods, ITEs did not occur evenly across different categories of conjoint probability. However, instead of occurring in areas where troops were more likely to encounter one another, ITEs more frequently occurred in areas of low conjoint probability; occurring in the conjoint probability category of 0-0.19 (least probability of encountering neighbouring troops) more frequently than any other category.

4.3 The Impact of ITEs on Intra and Intertroop Spatial Dynamics

ITE occurrence has been shown to have measurable impacts on patterns of space use. I aimed to test two predictions regarding the impact of ITEs on spatial patterns. Firstly, I hypothesized that the trajectory of troop movement will be impacted by ITE occurrence, with the study troops deflecting significantly from their original paths post-ITE. Contrary to my prediction, the study troops did not deviate significantly from their original trajectories post-ITE. While it is apparent that the troops moved away from each other post-ITE, there was no pattern in the deflection angles of the troops. The troops encountered one another other frequently and, when they did, neither troop was at a disadvantage as they used and exploited the area surrounding the encounter equally. Deflection angles did not differ from control angles as the troops had no home range to retreat to, given that the home ranges overlapped so extensively.

Second, I hypothesized that the spatial cohesion of RST and RBM would be impacted by the occurrence of ITEs, with the total extent of troop spread decreasing post-ITE. Counter to my prediction, intratroop spread did not change significantly after the occurrence of an ITE. Despite the frequent occurence of ITEs in this population, there is therefore no evidence that the occurrence of ITEs had any impact on the spatial patterns of the study troops.

4.4 Theory

According to competition theory, the greater the overlap in the use of a particular resource, the greater the competition for said resource (Butynski, 1990). Dietary overlap is, therefore, often used as an index for interspecific competition with territoriality mirroring seasonal fluctuations in food availability (Butynski, 1990; Moor & Steffens, 1972). While the dietary demands of our study troops clearly overlapped, the abundance of available resources across the foraging areas of all three troops would likely have limited the competition for food resources. Likewise, with large troop sizes, male competition for mates may have been less intense than observed in other populations.

These large troop sizes may also constrain the functionality of territoriality (Kavanagh, 1981). Territoriality is expected to constrain the size of a group as groups must inhabit areas small enough to be defendable, but large enough to support the survival of all group members (Kavanagh, 1981). In the case of our study troops, large group sizes may have inhibited territoriality, or territoriality may not have been functional for other reasons, such as extensive home range overlap or lack of limited resources, thus releasing the constraint of territoriality on group size. Similarly, when competitor density is extremely high, as appears to be the case in this population, defence may become uneconomical due to the associated high costs (Grant, 1993).

Despite the relatively low degree of territoriality displayed in this population, vervet females did cooperatively engage in aggression against neighbouring troop females. The role of males in territorial behaviour in this population, however, is less clear. Males have been reported to actively partake in intertroop aggression in other populations (e.g. Struhsaker, 1967a), but have rarely been observed to do so in this study population. Primate males have been reported to partake in resource defence when defending resources for females leads to greater reproductive success (Fashing, 2001).

4.5 Summary of Findings and Implications

To conclude, this population of vervets is distinct for its troop sizes, vervet density and greatly overlapping home ranges. The study population had home ranges that exceeded the sizes of those previously described (e.g. Struhsaker, 1967) and overlapped extensively. Territoriality is clearly limited in this population. While ITEs continue to occur at frequent rates, the competitive factors driving ITE occurrence were not clear. There was no evidence for defence of specific food patches or mate defence, nor did ITE frequency change with seasonal shifts. Evidence for home range defence was weak, with ITEs occurring across all areas of the home ranges. These troops are limited by space, but as there is an abundance of food, spatial defence is likely not favorable as resources are not defendable. This frequent occurrence of ITEs, however, had no impact on the spread of the troops, nor their trajectory. Territoriality is likely constrained or broken down in this population due to extensive overlap of home ranges, and the high density of vervets in the area. However, as the species is inherently territorial, they react when they encounter neighbouring groups, and fight, or ITE, in response.

In summary, the results described in this thesis suggest that the study population displays territorial behaviour that is less intense than the Amboseli population (Struhsaker, 1967), but perhaps more intense than the closely related Caribbean populations of *Clorocebus sabaeus* (Chapman & Fedigan, 1984). The population of *C. sabaeus* described in St. Kitts inhabit home ranges much smaller than those of our study population, with areas of overlap ranging from 3-31% of the total home ranges (Chapman & Fedigan, 1984). Despite the ability of the study troops to defend their home ranges, as suggested by the high defendability indexes, the population was not strongly territiorial. The relatively low degrees of territorial behaviour displayed in our study population may, conversely, be the result of high population density, and the limited exploitable habitat along the river valley. Future observations of this study population may allow for more comprehensive conclusions regarding the degree of territoriality displayed. However, the data appear to suggest that the expression of territoriality is not obligate, but variable and facultative, likely changing in response to continually varying and fluctuating environmental stresses.

As Lawes & Henzi (1995) state, using a “standard typological, bipolar construct” (p. 240) across a species is not accurate unless all populations, under distinctly diverse ecological pressures, have been observed to respond in the same fashion. If a species is categorized as territorial, territorial behaviour should be expressed regardless of varying ecological parameters. Yet, as Brown (1964) and Mitani and Rodman (1979) explain, intertroop aggression makes economic sense only under certain ecological conditions. Further, territoriality is much more complex than the territorial/non-territorial dichotomy it is often presented as; with territorial expression resulting from a combination of phylogenetic inertia and environmental adaptation (Chapman & Rothman, 2009). This research emphasizes that intraspecific variation in territorial behaviour is extensive and that each population should be examined within the context of its habitat. In the case of the vervet monkey, a species commonly labeled as territorial, cross-population observations support the notion that vervets are, instead, a species that display facultative territoriality, with territoriality emerging as a response to particular ecological parameters.

4.6 Future Research

This unusual study population, living at high density and in extensively overlapping home ranges, provides ample opportunity to investigate population dynamics and intertroop competition. In future, it would be particularly interesting to investigate male participation in ITEs. Males have been reported to actively participate in ITEs, herding females of their own troop and aggressively interacting with neighbouring troop members (Struhsaker, 1967b). Adult males in this study population, however, very rarely participated in ITEs, though their participation did appear to increase in the mating season (personal observations). Regarding intertroop dynamics, it would also be interesting to document all cases where the study troops observed a neighbouring troops but did not ITE. These data may shed more light on whether troops were, in fact, practicing active avoidance.

Additionally, it would be interesting to examine the effects of subgroup formation on territorial defence and the expression of territoriality. RST rarely formed a coherent group, subgrouping daily (unpublished data), and yet they continued to frequently engage in ITEs with neighbouring groups. Does subgroup formation support improved resource defence or is it simply a mechanism to cope with large group sizes, overlapping home ranges and high population density? Or perhaps, as Pasternak (2011) suggested, the subgrouping seen in RST is the beginnings of troop fission, which may occur when resources are sufficiently suitable to support an additional troop in the region.

Lastly, and more generally, a study of territoriality, especially facultative territoriality, would benefit greatly from long-term observations. Given the shifts we observed throughout the eighteen month study period, when resources appeared to remain abundantly available; shifts in home range boundaries and territorial behaviour in response to a lack of available water, which has been documented to occur at the Samara site (see McDougall, Forshaw, Barrett, & Henzi, 2010), would prove most interesting. With more available data, analysis at a smaller temporal scale may also be possible, and may reveal shifts in territorial behaviour not currently seen in the data.

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