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Social Behaviour and Crop Raiding in Chacma Baboons of the Suikerbosrand Nature Reserve

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A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science

Johannesburg

October 2010

Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree Master of Science to the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination to any other university.



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Govan Pahad
October 2010

Abstract

Conflict between baboons and humans is a common occurrence in many places where baboons exist in close proximity to cultivated land. This study examines patterns of raiding by baboons, farmer retaliation, and potential behavioural responses of baboons to that retaliation in and around the Suikerbosrand Nature Reserve, South Africa. Recent years have seen a rising baboon population and increasing complaints from farmers in the area about baboons raiding their farmland, leading to concerns that the population may have outgrown the resources available within the reserve.

This study consists of three parts: an examination of patterns of space use by baboons, using data from GPS collars fitted to one baboon in each of 10 troops in the reserve; an examination of the behaviour of baboons in 9 of these troops, using data gained though direct observation of troops within the reserve; and an examination of patterns of raiding and farmer retaliation, using data from questionnaires sent to land owners surrounding the reserve.

The data revealed that the troops appeared to be responding to resource scarcity and the opportunity to raid in a variety of ways. Some troops appeared to be raiding farmland intensively on short forays out of the reserve, while using the reserve as a refuge, indicated by small amounts of time spent outside the reserve, high levels of overlap between troops and low levels of foraging within the reserve. Other troops appeared to be shifting their home ranges out of the reserve to forage on fallow land, while also raiding farmland to some extent, indicated by large amounts of time spent outside the reserve, low levels of overlap between troops, and low levels of foraging within the reserve. Two of the troops studied apparently did not raid, as they never left the reserve.

Data from the questionnaires suggest that, while raiding is stimulated by food scarcity in the dry season, baboons raid maize and beans whenever available, seemingly preferring these crops over natural forage. While some farmers are responding to raiding with lethal retaliation against baboons, the effects of this on the social structure of the troops are unclear due to low sample sizes of behavioural data.

This study demonstrates some of the behavioural responses of baboons to raiding and farmer retaliation, and some of the different responses available to baboon troops facing a scarcity of natural food together with the opportunity to raid farmland. Based on my findings, I also provide recommendations to farmers and the Suikerbosrand management aimed at reducing baboon human conflict in the area.

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Animal Ethics clearance number: AESC2006/46/2A

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Chapter 1: Introduction

1.1 Chacma baboons

1.1.1 Appearance

Chacma baboons (*Papio hamadryas ursinus*) are a subspecies of savanna baboon, and are common throughout much of southern Africa. These large, diurnal, terrestrial monkeys have dog-like heads with deep-set eyes beneath prominent brow ridges, black, hairless muzzles and ears, and the males have razor sharp canines up to 5cm in length (Estes, 1991). Their fur is coarse, short and varies in colour (i.e. shades of dark brown, often blackish in patches, depending on the population; Estes, 1991; Smithers, 1983). Their limbs are long, sturdy and roughly even in length, with short, wide hands and feet with stubby digits, and their tails (approximately equal in length to their head and body) are held semi-erect (Estes, 1991; Smithers, 1983).

1.1.2 Habitat

Due to the benefits of their individual large size and strength, as well as their complex social structure (and the benefits of foraging efficiency and predator defence it provides), chacmas, like other savanna baboons, have managed to colonize the full range of savanna habitats between true grassland and true forest (Estes, 1991). However, they may also be limited by their need for refuges in which to sleep during the night, such as large, often thorny trees or high, rocky outcrops (Smithers, 1983) and by the availability of water (Hamilton, 1985).

1.1.3 Social organisation and social behaviour

Chacma baboon troops vary in size from less than 10 to approximately 200 individuals (Henzi et al., 1997). This allows for group defence against predators (Cowlishaw, 1994). It also promotes the cultural transmission of information (e.g. feeding habits; Camberfort, 1981).

Females remain in their natal group whereas males tend to disperse upon reaching adulthood (Weingrill et al., 2000) and will often change troop several times during their lives (Estes, 1991). Within a troop, access to food and, amongst males, to mates is determined by dominance hierarchies (Hamilton & Busse, 1982; Alberts et al., 2006). Female rank is fairly stable and is usually perpetuated trans-generationally due to maternal intervention in the

disputes of their offspring (Cheney, 1977). Male rank is more unstable, with high ranking males frequently losing their status to younger immigrants (Hamilton & Bulger, 1990).

Social cohesion is maintained by various affiliative interactions, the most noticeable of which is grooming, which is especially important in male-female and female-female relationships (Palombit et al., 1997; Barrett et al., 1999; Weingrill et al., 2000; Barrett et al., 2002). In male-female interactions, reciprocal grooming is used to establish temporary bonds during consortship (Weingrill et al., 2000) and during the infancy of a female's offspring, when male "friends" help to protect infants against infanticidal males (Palombit et al., 1997). Amongst females, grooming can be reciprocal or can be exchanged for other favours such as tolerance and reduced aggression from a more dominant female or being allowed to handle another female's infant (Barrett et al., 1999; Barrett et al., 2002; Henzi & Barrett 1999; Henzi & Barrett, 2002). Reciprocal grooming results in long term relationships between females, usually between close kin but sometimes between unrelated females of similar age or rank (Silk et al., 1999; Silk et al. 2006a; Silk et al. 2006b). The sociality of females has been found to positively correlate with infant survival (Silk et al., 2003).

Aggression is also a common and important feature of chacma baboon sociality and is used in the determination of rank by both males and females (Hamilton & Bulger, 1990; Cheney, 1977). Male-male aggression can be especially severe and can lead to damaging fights and even death (Brain, 1992). Females sometimes support close kin in conflict situations by vocalising their support (Wittig et al., 2007) or, more rarely, through physical intervention (Silk et al., 2004). Male chacmas, however, do not appear to form coalitions (Henzi et al., 1999), despite the presence of this behaviour in other subspecies of savanna baboon (Noë & Sluijter, 1995). Aggression by males against females and their infants is also common, although this is primarily associated with the rise to dominance of new, immigrant males (Pereira, 1983; Beehner et al., 2005). Rates of male-male aggression have also been found to increase during changes in the male hierarchy (Bergman et al., 2005).

There is evidence that the social behaviour of chacma and other savanna baboons is culturally acquired. For example, in one troop of olive baboons (*Papio hamadryas anubis*) living in the Masai Mara reserve of Kenya, a more peaceful social environment emerged after the most aggressive males in the troop were killed by an outbreak of bovine tuberculosis contracted from a rubbish dump. Ten years later, these behavioural conditions persisted even though none of the males present in the troop a decade earlier remained. New males joining the troop were therefore adopting its unique culture (Sapolsky & Share, 2004). In another study, chacma baboons in the Suikerbosrand Nature Reserve, South Africa, temporarily split

into subtroops during the winter, leading to more exclusive mating habits. Later, when the presence of a leopard in the reserve for several years prevented subtrooping, the tendency towards pair bonding remained, with males and females mating with fewer of the potential mates available than would normally be expected (Anderson, 1989).

1.1.4 Inter-and intra-troop dynamics

Troop size and organisation and inter-troop relationships are fairly flexible in baboons and are known to change in response to environmental pressures, indicating behavioural plasticity. Home range size has been found to increase with both troop size and resource scarcity (Barton et al., 1992). This influence of resource density means that the population density of chacma baboons can vary dramatically, from 3.5 baboons / km^2 in the Namib desert, Namibia, to 43.2 baboons / km^2 in the Okavango delta, Botswana (Hamilton et al., 1976).

Troop size also varies considerably due to fission-fusion processes, with chacma baboon troops ranging from 4 baboons in the Drakensberg, South Africa (Henzi et al., 1997), to 128 baboons in the Okavango delta, Botswana (Hamilton et al., 1976). Fission is generally driven by the withdrawal of low ranking females from a troop due to competition for food, or by males separating due to competition for mates (Ron, 1996). On the other hand, high predation pressure encourages baboons to remain in large troops for protection (Henzi et al., 1997). Barton et al. (1996) suggest that increased predation pressure should result in larger, multi-male groups for increased vigilance and predator defence, while increased within-group competition for food should result in groups with more conflict, grooming and coalitions between females, since female dominance hierarchies become more important for individual resource acquisition. Therefore, chacma baboons in areas of low predation pressure will break up into smaller troops to minimise within group competition for food, while those in areas of high predation pressure will form larger troops, where within group competition is likely to increase.

There is some empirical support for this hypothesis. In areas of the Drakensberg where predation pressure is low and resources are scarce, chacma troops fission at low numbers, forming troops containing an average of 22 individuals (Barton et al., 1996; Henzi et al., 1997), characterised by strong male-female bonds, with almost no female coalitions (Byrne et. al., 1990). In the Okavango Delta, however, where predation pressure is higher (Cheney et. al., 2004), troops contain an average of 79 individuals (Hamilton et al. 1976) and adult

females form strong kinship alliances based on well-differentiated grooming relationships (Silk et. al., 1999).

Chacma baboons are generally non-territorial between troops and have overlapping home ranges (Anderson, 1981). However, territoriality can develop under particular environmental conditions. Two troops living in a Namib Desert canyon formed a defended boundary near a waterhole and troops in the Okavango Swamp floodplain in Botswana, where resource and population densities were high, defended small territories along well defined boundaries (Hamilton et al., 1975; Hamilton et al., 1976). These studies suggest that chacma baboons can develop territorial behaviour when resource distribution or density favours resource defence.

1.1.5 Reproduction

Single infants are born after a six month gestation period (Smithers, 1983). Infants remain in constant contact with their mother for 6-8 months, after which they are weaned (Smithers, 1983). At first, the infant clings to its mother's underside, but later moves to her back and by two months it is able to walk, though it still usually rides on her rump (Estes, 1991). Yearling baboons are fairly independent, and even forage on their own, although mortality rates are high if the mother is killed, and it appears that young are dependent on the mother for up to two years (Estes, 1991).

Females become reproductively active by five years of age (Chance & Jolly, 1970). Males, though sexually mature by five years of age, can only compete with the larger males for access to females once they have grown to their full size and strength at seven to 10 years of age (Chance & Jolly, 1970).

Females have an average menstrual cycle of 36 days (Estes, 1991). The sexual skin of the female swells and becomes bright pink during oestrus to advertise their receptivity (Estes, 1991). This sexual swelling is at its maximum for 10 days of the cycle, fading 2-3 days after ovulation (Estes, 1991). Females usually start cycling again 10-12 months (minimum 5 months) after parturition and then go through about 4-5 non-receptive cycles before they can conceive again, resulting in a potential inter-birth interval of $1^1/_2$-2 years (Estes 1991). It has been found, however, that after periods of extreme heat or drought, female savanna baboons are less likely to cycle, less likely to conceive if they cycle, and less likely to have successful pregnancies if they conceive, and that females in larger groups were even less likely to conceive during droughts (Beehner et al., 2006), suggesting that the rate of reproduction can be depressed by high population density and adverse environmental conditions.

During the receptive phase of a female's cycle, she forms a temporary consort relationship (based on mutual grooming) with one or several males with whom she will mate frequently (Palombit et al., 1997; Weingrill et al., 2000). Male mating and reproductive success follows a rank based priority of access, which is related to both male dominance hierarchy and female choice, as females prefer high ranking males (Bercovitch, 1991; Weingrill et al., 2000). Lower ranking males will therefore usually only be able to mate if many females are receptive at once (Weingrill et al., 2000). This is even more pronounced in chacma baboons than in other savanna baboons, as lower ranking chacma males do not seem to form coalitions to compete with higher ranking males, as occurs in other subspecies of savanna baboons (Noë & Sluijter, 1995; Henzi et al., 1999).

Chacma males can be paternal but also have a tendency towards infanticide (Palombit et al., 1997; Weingrill, 2000). New immigrant males which rise to dominance often commit infanticide that causes lactating females to return to sexual receptivity, and may also induce miscarriage through harassment of pregnant females (Pereira, 1983; Beehner et al., 2005). Therefore, lactating females often form short term friendships with one or two of the males with which they mated, which then defend the infants from other, infanticidal males (Palombit et al., 1997). Female chacmas produce copulation calls which are louder and longer when they are closer to ovulation (Henzi, 1996) which may act to advertise the paternity of likely fathers, making them more likely to provide paternal care. In addition to reducing infanticide risk, other forms of paternal care include 'babysitting', which increases the survivorship of young, and intervening on behalf of offspring in agonistic disputes (Anderson, 1992; Buchan et al., 2003).

1.1.6 Mortality

Although the risk of predation seems to have a big influence on the behaviour of baboons and is considered to be one of the primary causes of group-living in baboons (Barton et al., 1996), it is uncertain as to whether predation has a significant impact on baboon populations, since direct evidence is not available (Cowlishaw, 1994). In 'Social Groups of Monkeys, Apes and Men', published in 1970, Chance and Jolly wrote “No direct attack [on savanna baboons] has been reported, except by a hyena on an isolated male” (pp. 70). However, Cowlishaw (1994) found considerable evidence for predation on baboons by drawing data from studies of the predators themselves, rather than of baboons, and found that the dominant predators of baboon populations across Africa were leopard (*Panthera pardus*), lion (*Panthera leo*) and hyena (*Crocuta crocuta*, *Hyeana brunnea*, *Hyaena vulgaris*) in order

of importance. Also mentioned as having been observed to attack and/or feed on baboons were chimpanzees (*Pan troglodytes*), domestic/feral dogs (*Canis familiaris*), silver backed jackals (*Canis mesomelas*), black eagles (*Aquila verreauxii*), tawny eagles (*Aquila rapax*), crocodiles and pythons (most likely Nile crocodiles, *Crocodylus niloticus*, and African rock pythons, *Python sebae*, though species names were not provided). In addition, Cowlishaw (1994) found that leopards, by far the most significant predators, are more likely to take adults than juvenile baboons and are more likely to take males than females. A recent study on chacmas in the Okavango Delta found that the majority of deaths among females and juveniles were due to predation (Cheney et al., 2004).

Infant mortality among baboons is often very high (Brain, 1992). Mortality of immature savanna baboons is highest when environmental conditions are unfavourable and mortality of immature females, in particular, is also higher when the troop size is large, especially for females born to low ranking mothers (Rhine et. al. 1988). This suggests that infant mortality is density dependant. The primary causes of infant mortality among chacma baboons include tick infestation, kidnapping by adult females (Brain, 1992) and infanticide by adult males (Tarara, 1987; Cheney et al., 2004).

While no reports of adult females being killed by other baboons could be found, males often die from canine inflicted wounds during male–male aggression (Brain, 1992).

In areas where baboons come into contact with humans, they face added dangers. Baboons living near agricultural land often raid farms, which can result in lethal retaliation from farmers (e.g. shooting, trapping and poisoning; Chance & Jolly, 1970; Naughton-Treves, 1997; Holmern et al., 2007). Another potential danger associated with human activity is roadkill. For example, a study in Tanzania found that roadkill accounted for 10% of annual mortality in a troop of yellow baboons (*Papio hamadryas cynocephalus*; Drews, 1995).

1.1.7 Anti-predator behaviour

At night, baboons sleep in trees or on cliffs to avoid predators (Chance & Jolly, 1970). While out foraging during the day, baboons are very vigilant, especially when moving through cover that could conceal a predator, during which times tension increases within the group, resulting in an increase in vigilance and group cohesion (Altmann & Altmann, 1970). If danger is detected, a warning bark is issued to alert the troop (Estes, 1991). Baboons will climb trees and rocks to escape danger when possible but will also mob predators and have been documented killing leopards (Estes, 1991) and even ganging up against lions (Saayman, 1971).

The foraging behaviour of baboons is also sensitive to predation risks. Baboons may avoid a particular area or become hypersensitive to danger signals in an area as a result of a recent experience with a predator, and repeated experiences may result in more long term shifts in habitat preference and avoidance (Altmann & Altmann, 1970). In a study of a desert population of chacma baboons, individuals spent more time in relatively low risk, food poor habitats and less time in relatively high risk, food rich habitats than would be expected based simply on ideal free distribution, indicating a modification of foraging habits based on the fear of predation (Cowlishaw, 1997a); resting and grooming were also reserved almost exclusively for the low risk habitats. In another study, these baboons used refuges intensively where available, but in areas where refuges were scarce they foraged and then left the area as quickly as possible (Cowlishaw, 1997b).

1.1.8 Foraging

Chacma baboon foraging behaviour and diet are incredibly diverse. They have been recorded eating grasses, seeds, roots, leaves, flowers, bark, gums, mushrooms, fruits, pods, shoots, bulbs, tubers, lizards, insects, spiders, scorpions, ants, slugs, hares, the young of small antelope, shellfish (on the Cape Peninsula) as well as raiding farmland for agricultural crops such as maize, sorghum and peanuts, orchard crops such as pawpaws and bananas and even domestic animals such as chickens, lambs and young goats (Smithers, 1983). Again, in foraging, as in other aspects of baboon ecology, learning from others in the social group is important for foraging (Camberfort, 1981). One study found that once a new food source has been discovered, most commonly by juveniles, the discovery spreads rapidly through the rest of the troop (Camberfort, 1981). In another study, adults prevented younger individuals from accessing fruit experimentally drugged with cynalin until it was ignored altogether (Fletemeyer, 1978).

In a study of the Suikerbosrand baboons over the same period as this study, Segal (2008) found that baboons had a broad diet in the dry season (a mix of fruit and seeds, plant matter, invertebrates and maize) but had a narrower diet at other times of the year, relying primarily on new leaf growth in the early rainy season and on fruit and seeds in the late rainy season.

1.2 Raiding

1.2.1 Baboons and other large mammals as pests

Large mammals will often forage on agricultural land, and human-animal conflict is a common problem in many places where farmland abuts protected or otherwise natural land, most notably throughout Africa and Asia (Sukumar, 1990; Naughton-Treves, 1997; Kharel, 1997; Hoare, 1999). In Asia, large mammals that feed on crops and livestock include primates, such as maroon langurs (*Presbytis rubicunda*), long-tailed macaques (*Macaca fasicularis*), pig-tailed macaques (*Macaca nemestrina*) and orang-utans (*Pongo pygmaeus*); carnivores such as sun-bears (*Helarcto malayanus*), Himalayan black bears (*Ursus thibetanus*), leopards (*Panthera pardus*), civets (*Paradoxurus* sp.), leopard cats (*Felis bengalensis*) weasels/ martens (*Mustela* sp.) and otters (*Lutra* sp.); ungulates such as bearded pigs (*Sus barbatus*) and sambar deer (*Cervus unicolor*); and porcupines (*Hystrix brachyura*) and Asian elephants (*Elephas maximus*) (Kharel, 1997; Salafsky, 1993; Sukumar, 1990). In Africa, livestock predation is primarily due to baboons (*Papio hamadryas*), leopard, lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) (Butler, 2000; Kolowski & Holekamp, 2006; Holmern et al., 2007), while the main species for the raiding of agricultural land are African elephant (*Loxodonta africana*), primates such as baboons, redtail monkeys (*Cercopithecus ascanius*), vervet monkeys (*Cercopithecus aethiops*), and chimpanzees (*Pan troglodytes*) and bushpigs (*Potamochoerus* sp.), with antelope species such as red duiker (*Cephalophus* sp.) and bushbuck (*Tragelaphus scriptus*) and crested porcupines (*Hystrix africae-australis*) also contributing to the problem (Naughton-Treves, 1997; Naughton-Treves et al., 1998; Hoare, 1999; Saj et al., 2001; Sitati et al., 2003).

Therefore, baboons are known to be responsible for feeding on both livestock and crops. Livestock predation due to baboons is considerably varied. In Gokwe communal land in Zimbabwe, chacma baboons were found to be responsible for 52% of the livestock killed, with lions and leopards responsible for 34% and 12% respectively (Butler, 2000). In villages adjacent to the Serengeti National Park, Tanzania, yellow baboons were only responsible for 0.4% of kills, with spotted hyenas responsible for 98% (Holmern et al., 2007); and in villages adjacent to the Masai Mara National Reserve, Kenya, baboons were not known to take livestock at all (Kolowski & Holekamp, 2006). Where baboons do predate on livestock, they generally take chickens, lambs and young goats rather than the adult sheep and cattle that lions and leopard are known to kill (Smithers, 1983; Butler, 2000).

Raiding of crops by baboons is more common. Olive baboons are known crop raiders, and several studies of raiding around the forest reserves of Kibale National Park and Budongo

Forest Reserve in Uganda provide information about their preferences (Naughton-Treves, 1997; Naughton-Treves et al., 1998; Hill, 2000). Olive baboons were not only considered to be the worst crop raiding animals by farmers around Kibale, they were also responsible for the greatest overall area of crop damage (Naughton-Treves, 1997). The most favoured crop of these baboons was found to be maize, followed by sweet potatoes and then groundnuts (Naughton-Treves, 1997). These baboons fed on maize throughout its life cycle, eating seedlings, inflorescence, pith and fruit, and would feed on the fruit when available, regardless of the abundance of forest fruit (Naughton-Treves et al., 1998). They also fed on a greater variety of crops than other primates, taking root and tuber crops that other primates ignored (Naughton-Treves et al., 1998).

Chacma baboons are also known as crop raiders (Falls, 1993). Around Kibale National Park, Uganda, crop losses to olive baboons were confined almost entirely to within 200m of the forest edge (Naughton-Treves, 1997) while around the Suikerbosrand Nature Reserve, South Africa, chacma baboons cause damage on farmland and in towns up to 40 km from the reserve (Falls, 1993). This is most likely because the forest-farmland border (Kibale) is a more severe edge than the savanna-farmland border (Suikerbosrand), allowing the chacmas to roam farther from the reserve in relatively familiar habitat.

The raiding behaviour of large mammals can be viewed as an extension of their foraging strategies (Sukumar, 1990). Carnivores have been found to take more livestock at times when prey densities are low in their natural environment (Kolowski & Holekamp, 2006) and crop raiders such as primates and elephants are known to shift to foraging on agricultural land when crop availability provides improved foraging opportunities (Naughton-Treves et al., 1998; Sukumar, 1990).

Although natural food scarcity, overpopulation and the intrusion of agricultural land are thought to provide incentives to large mammals, such as elephants and primates, to raid farmland or to increase the level of raiding, large mammals are also known to continue raiding farmland even when natural forage is not scarce, due to the higher productivity, palatability and nutritive value of crop species compared to wild plants (Sukumar, 1990; Falls, 1993; Strum 1994; Naughton-Treves et al., 1998). In a study of crop raiding by olive baboons, redtail monkeys and chimpanzees around Kibale National Park, Uganda, it was found that all three species raided banana plantations less often when forest fruit was plentiful, but would take maize whenever it was available, regardless of natural fruit availability (Naughton-Treves et al., 1998). This suggests that maize was more appealing to these baboons than any natural alternative, perhaps due to its high carbohydrate content. It also suggests that, when

equally valuable wild alternatives are plentiful, such as with the fruit, baboons would rather not raid. This may be due to the threat of 'predation' from farmers.

In another study, troops of olive baboons that did not have previous experience with human food generally appeared very reluctant to raid, despite the expansion of agriculture in the area (Strum, 1994). These troops responded to the loss of natural foraging land in a variety of ways, from enlarging or shifting home ranges or reducing troop sizes to raiding as a backup strategy or raiding as the primary foraging strategy (Strum, 1994). This suggests a flexible response to raiding behaviour, with different troops responding to the same situation in different ways.

On a global scale, crop losses due to large mammals are insignificant compared to those caused by invertebrates and rodents (Naughton-Treves, 1997). On a local scale, however, crop losses due to large mammals can be a serious problem for the livelihood of farmers, especially small land holders and subsistence farmers (Naughton-Treves, 1997). A study on crop losses to large mammals around Kibale National Park, Uganda found that these losses only amounted to 7% of planted fields within 450 metres of the park boundary, but, due to the localised nature of raiding events, 7% of farmers lost over 50% of their planted maize and cassava (Naughton-Treves, 1997). Such losses naturally lead to bad feelings among farmers towards the animals responsible, and often towards the parks that protect them (Kharel, 1997; Naughton-Treves, 1997). Baboons are often considered dangerous as well as just crop raiders and were described as crafty and a menace to women and children by farmers around Kibale (Naughton-Treves, 1997). Foraging on farmland by large mammals therefore often results in lethal retaliation (Falls, 1993; Naughton-Treves, 1997; Holmern et al., 2007). Not surprisingly, greater losses to raiding animals leads to an increase in the approval of lethal retaliation, while effective steps to reduce raiding have been found to lead to a reduced desire for retaliation (Holmern et al., 2007).

1.2.2 Potential effects of raiding and farmer retaliation on baboon troops

Foraging in areas of human land use can expose baboons to a range of dangers such as cars (Drews, 1995), new diseases (Sapolsky & Share, 2004), domestic dogs (Cowlishaw, 1994) and humans themselves (Naughton-Treves, 1997; Falls, 1993). Foraging on agricultural land has been found to increase growth and reproduction due to increased foraging efficiency and food quality, and to increase death and injury due to retaliation from farmers (Strum, 1994). Farmers will often shoot baboons (Falls, 1993) and will use traps, snares and poison to kill baboons foraging on their land (Naughton-Treves, 1997).

Shooting can also alter the composition of baboon troops (Chance & Jolly, 1970). This can have potentially serious implications for the troop, especially if farmers target large males, thereby frequently removing the alpha males and shifting the demography of the troop to be more female biased. It has been found that male savanna baboons prefer to immigrate into troops that have a higher proportion of females than the population average (Henzi et al., 1998). A troop that constantly loses adult males could therefore experience an increase in immigrant males. This is likely to increase aggression within the troop, as immigrant males not only alter the troop's existing dominance hierarchy (Hamilton & Bulger, 1990), leading to an increase in male-male aggression (Bergman et al., 2005), they also often use infanticide as a reproductive strategy (Busse & Hamilton, 1981). It has also been found that male baboons in troops with relatively few males will often aggressively herd females and infants away from other troops to prevent new males from joining (Henzi et al., 1998).

1.2.3 Stress

Despite its advantages, social living can also be a source of stress in many primate species (Abbott et al., 2003). This is often assessed by the measurement of glucocorticoid hormones in faecal samples. In chacmas, changes in the male hierarchy (which also correlated with increased male-male aggression) have been found to increase glucocorticoid levels in males (Bergman et al., 2005) and the rise to dominance of immigrant males has been found to increase glucocorticoid levels in lactating and pregnant females, especially in those that did not have male “friends” to guard against infanticide (Beehner et al., 2005). Increased glucocorticoid levels were also found in females that lost close kin to predation (Engh et al., 2006). While such stress occurs naturally within baboon troops, it is likely to be increased if retaliation from farmers increases mortality and rank instability within a troop.

Responses to stress generally involve some sort of displacement / self directed behaviours. Maestripieri et al. (1992) found that scratching, self-grooming, yawning and body shaking were the most commonly reported displacement activities in non-human primates, and that these tended to occur in situations of psycho-social stress. Castles et al. (1999) found that these same behaviours plus self touching can be used as a measure of relationship uncertainty in female olive baboons. Interestingly, females which were stressed due to the loss of close kin responded by increasing their rate of social grooming and number of grooming partners (Engh et al., 2006). While this could be seen as an attempt to replace lost social alliances, it has also been suggested that social grooming, especially amongst close kin, can reduce stress levels in primates, as subordinates in primate species that have opportunities for

social support have lower levels of the stress hormone cortisol than those that do not (Abbott et al., 2003).

1.3 Baboons at Suikerbosrand Nature Reserve and rationale for this study

The Suikerbosrand Nature Reserve (hereafter referred to as Suikerbosrand) is a small nature reserve with adjoining farmland, situated in close proximity to several residential areas. Chacma baboons, the only non-human primates on the reserve, are frequently seen in the areas surrounding the reserve and complaints are often received from farmers that their farms are being raided by baboons (Falls, 1993). The baboons are also becoming problematic at camp sites within the reserve where they raid dustbins and steal food. This increase in foraging in farmland and areas of human habitation has lead to concerns that the baboon population may have grown too large to be sustained by the food available naturally within the reserve, especially since there are almost no natural predators of baboons present in the reserve. Baboons can utilise a wide variety of natural foods, including plants, invertebrates and small vertebrates (Smithers, 1983). It is feared that an unnaturally high population density maintained by a partial reliance on food acquired from humans will adversely affect the plant and animal species diversity of the reserve, the maintenance of which is one of the primary goals of the management of Suikerbosrand according to their tourist brochure (Gauteng Nature Conservation, 1997). It is also possible that a reliance on raiding and aggressive retaliation from humans (such as the shooting of baboons by farmers) may have negative effects on the behaviour of the baboons. Another concern is the possibility of injury to people if interactions between humans and baboons continue. The Suikerbosrand management is therefore eager to find an appropriate strategy to manage the baboon population or to restrict their raiding behaviour.

Historically, baboons in the Suikerbosrand area were contiguous with baboon populations across the highveld (Falls, 1993). However, when Voortrekker farmers settled in the area around 1850, they regarded the baboons as pests and actively hunted them in an effort to exterminate the problem (Falls, 1993). Baboons in the area only survived in the interior of what is now the Suikerbosrand Nature Reserve as it was too mountainous for agriculture (Falls, 1993). The baboon population in the Suikerbosrand has therefore been isolated for at least 100 years, with the closest neighbouring population today being in the Magaliesburg, about 150 km away (Falls, 1993). The reserve was declared in 1972, protecting the baboons in the Suikerbosrand and allowing their population to grow (Falls, 1993). While baboons have always raided farmland close to Suikerbosrand, there has been an increase in the number of

complaints since 1992, as well as complaints from farmers that did not previously have baboons on their land (Falls, 1993). This may be due to a reduction in the number of live-in farmers compared to weekend and tenant farmers, which may have resulted in farms being less well guarded, making raiding an easier option for baboons. Suikerbosrand management have also suggested that overpopulation may be forcing the baboons to raid farmland (J. Hennop, pers. comm.).

Falls (1993) provided a population graph for baboons in the Suikerbosrand, based on earlier censuses from 1974. He suggested that after a period of exponential growth, the population had stabilised at around 650 baboons. However, a 2006 census of the baboon population carried out by the Suikerbosrand management estimated that the population had since grown to around 770 (Figure 1). If Falls (1993) was correct, it seems that an increase in foraging outside the Suikerbosrand has allowed the population to increase beyond the carrying capacity of the reserve. Another possibility however, is that the population has been increasing steadily since the early 1980s.

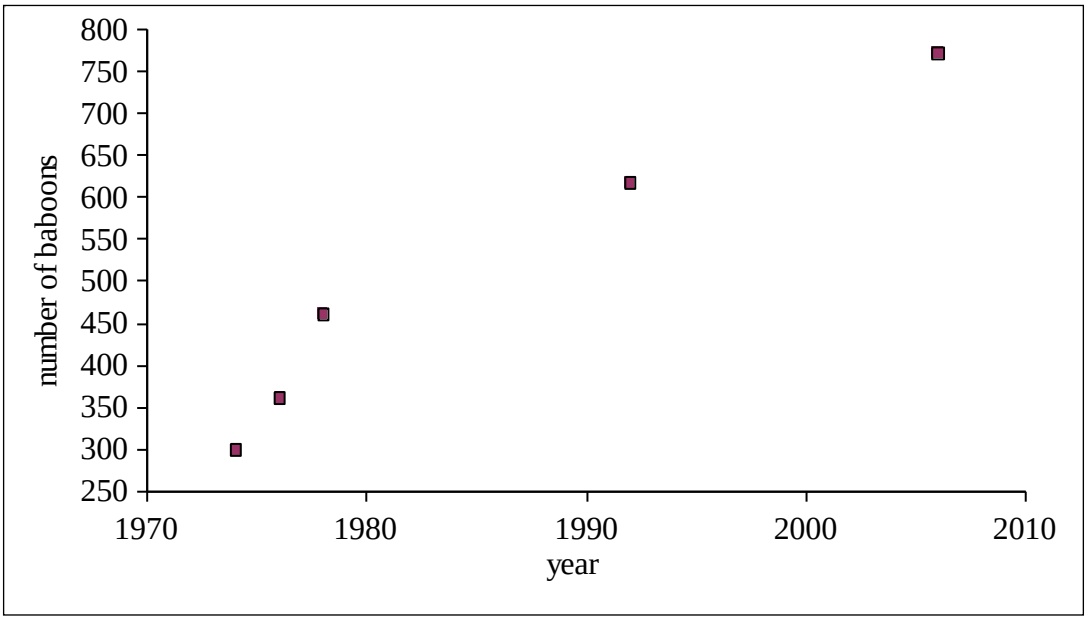


Figure 1 Chacma baboon population sizes in the Suikerbosrand Nature Reserve from its proclamation (1972) to the last census (2006).

In an effort to better understand the biology of the baboons, the Suikerbosrand management fitted selected baboons with cell-phone telemetry collars in order to track the movement of the troops. There are also channels of communication open between the reserve management and farmers in surrounding areas (J. Hennop, pers. comm.), making it possible

that the farmers will be willing to provide information from their perspective about the baboon pest problem. This provided a valuable opportunity to examine baboon raiding behaviour in more detail than is normally possible.

1.4 Aims

I studied the chacma baboons in the Suikerbosrand Nature Reserve to ascertain which troops were raiding farmland, reasons for their raiding farmland, and what affect raiding was having on their social behaviour.

My study had three broad areas of investigation.

1. Space use. I used information from the GPS collars and a census to examine space use by the chacma baboon troops over a year (March 2006 to February 2007). In particular, I measured several parameters: time spent outside the reserve, troop size, monthly space use area, monthly space use overlap with other troops and seasonal shifts in space use to assess which troops are raiding farmland, and which troops, if any, are leaving the reserve due to resource scarcity.
2. Behaviour. I observed the behaviour of raiding and non-raiding troops (classified based on the space use data) inside the reserve to detect differences between them. The aim was to establish the effects of raiding and farmer retaliation on the social behaviour of raiding troops.
3. Farmers. I used questionnaire surveys to obtain responses from farmers about their losses to baboons, patterns of raiding and responses of farmers to raiding. The aim of was to investigate how much raiding is taking place, the seasonality of raiding and preferred crops of the baboons, as well as to assess the levels of farmer retaliation to the baboons.

1.5 Hypotheses and predictions

For the GPS data on space use and the behavioural data, hypotheses concerning the implications of parameters examined are given, the basis for them is explained and several resulting predictions are given.

1.5.1 Space use

General patterns of space use by baboon troops should give an indication of which troops are raiding farmland. Various predictions can be made based on the assumption that

farmland provides improved foraging opportunities at the cost of increased risk from farmers. The basis for these predictions is outlined below.

Time outside

Time spent outside the reserve will identify troops that leave the reserve and thus have the opportunity to raid. Leaving the reserve, however, does not necessarily mean that a troop is raiding farmland. As much of the land around the reserve is not actually cultivated, some troops may be foraging on fallow land around the reserve rather than on cultivated farmland. These troops would still be exposed to many dangers not present in the reserve and since baboon troops tend to avoid high risk areas as much as possible (Altmann & Altmann, 1970; Cowlishaw, 1997a & b), they should have no incentive to risk venturing outside unless resources were scarce inside the reserve, perhaps suggesting that the baboon population has grown too large for the reserve to support.

Troops may also raid farmland but spend relatively little time outside the reserve. Troops that are raiding farmland are likely to use the reserve as a refuge, foraging on farmland as quickly as possible and then retreating to the reserve for other activities such as rest and socialising. This is a documented response of chacma baboons to areas which are both dangerous and resource rich (Cowlishaw, 1997b). Therefore, if troops are raiding farmland close to the reserve, they may still spend most of their time inside the reserve.

Seasonal patterns

The amount a troop shifts spatially during the year and the seasonal patterns in the amount of time it spends outside the reserve will help to reveal the foraging strategies of the troop. Troops that are managing to find enough food in one area throughout the year will not have to shift their location. Troops that are raiding farmland seasonally and / or leaving the reserve seasonally to avoid periods of food scarcity within the reserve will shift spatially to a larger extent over the year.

Evidence that troops spend more time out of the reserve in the early dry season when maize (the main crop grown around the reserve) is ripe will suggest that troops are leaving the reserve to raid farmland. On the other hand, evidence that more time is spent outside the reserve during the late dry season (when resources are most scarce) will suggest that troops are leaving the reserve at least partly owing to resource scarcity.

Troop size

Baboons form larger troops under higher predation pressure to increase vigilance and group defence (Barton et al., 1996; Henzi et al., 1997), and therefore raiding troops are expected to be larger than non-raiding troops. Also, the availability of plentiful agricultural food should reduce within group competition for food, one of the primary causes of fission of troops (Ron, 1996).

Monthly space use area and overlap

Home range size depends strongly on the availability of resources (Barton et al., 1992). The increased density of food resources on agricultural land should therefore allow baboon troops that are raiding farmland to decrease their monthly space use area and / or to increase their monthly space use overlap with other troops. They may also overlap more with other troops at times of the year when they spend more time outside the reserve, assuming that more time outside the reserve indicates more raiding.

Troops that are leaving the reserve due to overpopulation and are not raiding farmland, on the other hand, would be expected to take advantage of the lower density of baboons outside the reserve by using larger areas of land and / or overlapping less with other troops. These troops may also overlap less with other troops at times of the year when they spend more time outside of the reserve.

Predictions

1. Raiding troops will spend more time outside the reserve in the early dry season when maize ripens. They will be larger than non-raiding troops and will have smaller monthly space use areas and / or will overlap more with other troops. They should overlap even more with other troops at times of the year when they spend more time outside the reserve. They will also shift their location more throughout the year than troops that do not leave the reserve.
2. Troops that are leaving the reserve due to resource scarcity will spend more time outside the reserve in the late dry season. They will be larger than troops that do not leave the reserve. If they are not also raiding farmland they will have larger monthly space use areas and / or will overlap less with other troops and they should overlap even less with other troops at times of the year when they spend more time outside the reserve. They will also shift their location more throughout the year than troops that do not leave the reserve.

3. Non-raiding troops that do not leave the reserve will be smaller than other troops and will have intermediate monthly space use areas and overlaps with other troops (intermediate meaning between raiding troops and troops foraging on fallow land). They will shift their location less throughout the year than other troops.

1.5.2 Behaviour

Behavioural differences between raiding and non-raiding troops will provide an indication of how troops are responding to raiding and farmer retaliation. Various predictions can be made based on the assumption that farmland provides improved foraging opportunities at the cost of increased risk from farmers. The basis for these predictions is outlined below.

Aggression

The shooting of baboons (especially large males) by farmers is likely to disrupt the social hierarchy, which is known to result in increased aggression within a troop (Pereira, 1983; Beehner et al., 2005; Bergman et al., 2005). Aggression should therefore be more frequent in raiding troops than in non-raiding troops.

Vigilance

Although vigilance is known to increase as a result of predation, this tends to be area specific, with baboons being more vigilant in areas where they have previously experienced predation (Altmann & Altmann, 1970). Also, Cowlishaw (1997b) found that chacmas are a lot less vigilant in a refuge than away from it. Therefore, dangers experienced outside the reserve will not necessarily result in an increase in vigilance within the reserve.

Self-grooming

Glucocorticoid levels (an indicator of stress) increase in male and pregnant and lactating female baboons in response to changes in the social hierarchy and the associated increases in aggression (Beehner et al., 2005; Bergman et al., 2005). Glucocorticoid levels also increase in female baboons that have lost close kin (Engh et al., 2006). As self-grooming is thought to be an indicator of stress in primates (Maestripieri et al., 1992) and has been found to indicate relationship uncertainty in olive baboons (Castles et al., 1999), it should be more frequent in raiding troops than in non-raiding troops due to the loss of individuals and the increased social instability.

Foraging

If raiding troops are using the reserve as a refuge, they should spend more time resting and socialising inside the reserve, with a large proportion of their foraging taking place outside the reserve (Cowlishaw, 1997a). Also, as the density of food is far higher on agricultural land than on non-agricultural land, troops that are foraging on farmland should need to spend a lot less time foraging overall. Foraging should therefore be less frequent inside the reserve in raiding troops than in non-raiding troops.

Socio-positive behaviour

Social grooming, the primary component of socio-positive behaviour, can potentially be affected by many factors, such that a simple response to raiding and farmer retaliation is unlikely. If troops are using the reserve as a refuge, social grooming might be expected to be more common in raiding troops when inside the reserve due to this behaviour occurring more in low risk areas (Cowlishaw, 1997a). Also, female baboons respond to the loss of grooming partners by increasing social grooming of others (Engh et al., 2006). On the other hand, increased food availability may reduce female-female grooming as within group competition for food is thought to be the main cause of female-female grooming and coalitions (Barton et al., 1996). Overall, therefore, no major differences in social grooming can be predicted between raiding and non-raiding troops.

Motor play

Play behaviour is known to decrease due to poor habitat quality and food shortages in gelada baboons (*Theropithecus gelada*; Barrett et al., 1992) and in langur monkeys (*Presbytis entellus*; Sommer & Mendoza-Granados, 1995). Play may therefore be lower in non-raiding baboons if the natural food availability in the reserve is low. Play may also increase in raiding troops if it is a behaviour reserved for low risk areas, as argued for grooming (above). However, Cowlishaw (1997a) did not look at play behaviour in his study. Also, it is unknown what the effects of social instability are on play behaviour. Therefore, no differences in motor play can be predicted, especially since the low levels of this behaviour will make any trend very difficult to detect.

Mating

Foraging on agricultural land has been found to increase growth and reproduction due to increased foraging efficiency and food quality (Strum, 1994). Also, new immigrant males

which rise to dominance often commit infanticide to cause lactating females to return to sexual receptivity, and may also induce miscarriage through the harassment of pregnant females (Pereira, 1983; Beehner et al., 2005). Both of these trends should increase the amount of time females spend in the receptive phase of their reproductive cycles in raiding troops, thereby increasing the amount of mating in these troops. Levels of mating are therefore predicted to be higher in raiding troops than in non-raiding troops.

Prediction

Inside the reserve, troops that raid farmland will have higher levels of aggression, self-grooming and mating and lower levels of foraging than troops that do not raid farmland.

1.5.3 Responses by farmers

As the questionnaires provide largely qualitative data, specific predictions will not be made. However, based on other studies of baboon-farmer conflict (Naughton-Treves, 1997; Naughton-Treves et al., 1998), it is expected that maize farmers will be particularly affected by baboons, and that this is likely to result in lethal retaliation. It is also expected that raiding will increase during the early dry season when maize ripens and during the late dry season when natural food is scarce, as baboons have been found to increase raiding due to both natural food shortages and the availability of preferred crops such as maize (Naughton-Treves et al., 1998).

Chapter 2: Materials and methods

2.1 Study site (Much of the information provided here was obtained from a tourist brochure: Gauteng Nature Conservation, 1997).

This study was conducted over a year from March 2006 to February 2007 at the Suikerbosrand Nature Reserve (Figure 2). The Suikerbosrand Nature Reserve is a protected area of 133 km^2 situated about 50 km south of Johannesburg. The reserve is surrounded by commercial farmland (J. Hennop, pers. comm.). The reserve ranges between 1545-1917 m above sea level, and is dominated by the Suikerbosrand mountain range. The average rainfall is between 650-700 mm per year and the temperature varies from 10 to 32 °C in summer and from 0 to 20 °C in winter. There is a range of vegetation types in the reserve, with grassland dominating the mountain slopes and plains, and wooded patches common in the gorges. The eastern edge of the reserve is mainly protea veld and there is an area of Acacia forest in the south west corner, as well as patches of aloe forest scattered throughout the mountain slopes. Rocky outcrops are very common among the mountain slopes and peaks. There is a vlei in the south, a dam of about 200 by 100 m in the east, and several perennial rivers as well as permanent water sources (provided for the wildlife) scattered throughout the reserve. An area of land adjoining the northern edge of the reserve (an additional 65 km^2) was purchased from farmers from 2002 to 2004 and is being left to return to a wild state through natural succession (J. Hennop, pers. comm.). During the period covered by this study, the existing fence was not removed to incorporate this new land. 2006 was a comparatively wet year, with 713 mm of rainfall.

Gauteng Nature Conservation (1997) lists the large mammals present in the reserve as eland, kudu, red hartebeest, zebra, black wildebeest, blesbok, oribi, leopard, brown hyena, black backed jackal, baboon, porcupine, springbuck, reedbuck, grey rhebuck, mountain reedbuck, common duiker, steenbok, aardwolf, silver fox, mongoose, genet and aardvark. Although leopards are listed as present, no sign of leopard has been seen in the reserve for over a decade (J. Hennop, pers. comm.). Gauteng Nature Conservation (1997) also lists black eagles, a predator of baboons (Cowlishaw, 1994), as present in the reserve. In fact, there was a single pair of black eagles in the reserve (J. Hennop, pers. comm.). Therefore, although there are many potential competitors of baboons, there are no potential predators other than brown hyena and a pair of black eagles. Natural predation of baboons in the reserve is therefore low if present.

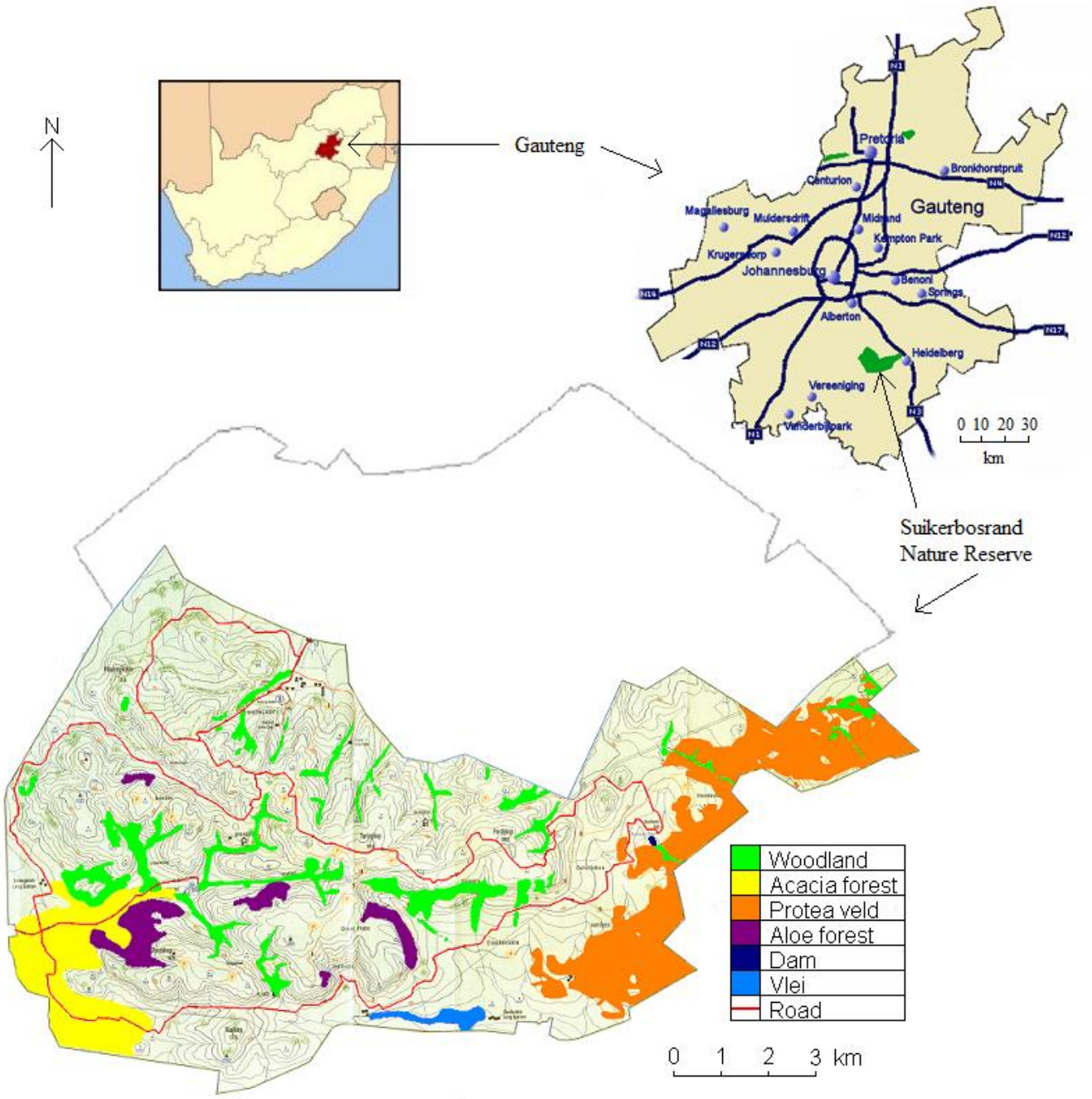


Figure 2 Top: Maps showing the location of Gauteng Province (in red) in South Africa (Wikipedia) and the Suikerbosrand Nature Reserve (in green) in Gauteng (adapted from a map of Gauteng from http://www.findandstay.co.za). Bottom: Map of the Suikerbosrand Nature Reserve showing habitat types (adapted from a tourist map; Gauteng Nature Conservation, 1997) with wooded areas in green, Acacia forest in yellow, Protea veld in orange, aloe forest in purple, the dam in dark blue, the vlei in light blue and the tourist route in red. The remainder of the reserve is grassland. The new land to the north has been left blank.

2.2 Cell-phone telemetry collars

Towards the end of 2005, the Suikerbosrand Nature Reserve management, together with the Gauteng Department of Agriculture, Conservation, Environment and Land Affairs, set out to collar 12 baboons (1 in each of the 12 troops in the reserve) with cell-phone telemetry collars purchased from Africa Wildlife Tracking (www.awt.co.za). For each troop, a sample of about 5 to 10 baboons were caught in cage traps baited with vegetables. An adult female was fitted with a cell-phone telemetry collar; females were selected as they are less likely than males to change troops (Weingrill et al., 2000). The cell-phone telemetry collars use a GPS (global positioning system) to calculate co-ordinates in degrees latitude and longitude. These co-ordinates are sent via SMS to a GSM network. The data were accessed via the Africa Wildlife Tracking website www.yrless.com. The collars were only active during the day and the time interval between SMSs was set to 4 hours to conserve the battery life of the collars. When cell-phone coverage was unavailable, each collar could store up to 240 GPS co-ordinates to be sent off as soon as coverage improved (i.e. when collared individuals were within the range of a cell phone mast). The collars had a battery life of approximately 18 months.

2.3 Baboon census

In October 2006, I participated in a census of the baboon population conducted by the Suikerbosrand management. The technique used was a known group count (Matthews, 2005) in which the radio telemetry collars were used to guide teams of counters to each of the troops. The teams would then follow the troops until they had a clear view to count as many of the individuals as possible.

2.4 Space use

2.4.1 Data Collection

The space use of the baboons was monitored using the GPS data provided by the collars. For each troop, the movement of the female fitted with the collar was used as a surrogate for the movement of the whole troop. GPS coordinates for one year (March 2006 to February 2007) were downloaded from the Africa Wildlife Tracking website www.yrless.com.

ArcMap9 (ESRI 2004) a GIS software package, was used to overlay the GPS co-ordinates of the troops onto a map of the Suikerbosrand and surrounding areas and Hawth's Analysis Tools© (Beyer 2004) were used to analyse the data in ArcMap9. The Count Points in Polygons tool was used to obtain the percentage of each troop's GPS co-ordinates that fell

inside the reserve. This information was used as an estimate of the percentage of time each troop spent inside the reserve. The Create Minimum Convex Polygons tool was used to generate home ranges for the troops. This tool constructs the smallest possible convex polygon around a collection of points (in this case, the GIS co-ordinates for each troop). This method was used since the areas utilised by the troops were convex. Because the areas utilised by the troops shifted substantially throughout the year, they were calculated separately for each month so as to provide a more accurate indication of the actual surface area being used by the troops at any one time. The Polygon in Polygon Analysis tool was used to calculate the percentages of space use overlap between troops for each month. The same tool was used to calculate the percentages of space use overlap between each troop and itself during different months. This provided a measure of the degree to which each troop shifted its space use area during the year.

2.4.2 Data analysis

The total percentage of time spent inside and outside the reserve by different troops in Suikerbosrand Nature Reserve was used to identify the troops that had opportunities to raid farmland and troops were grouped into categories (leavers, non-leavers and occasional leavers) based on this result. The percentage of time spent outside the reserve each month by leavers and occasional leavers was analysed using Friedman tests to assess when during the year troops representing these categories spent the most time outside the reserve.

Troop size (from the census) was compared to leaving category using a Spearman's rank correlation to ascertain whether leaving correlated with an increase in troop size.

The mean monthly space use areas of the troops were compared to leaving category using a Spearman rank correlation to ascertain whether leaving correlated with a decrease in monthly space use area.

The mean monthly space use overlaps of the troops were compared to leaving category, using a Spearman rank correlation to establish whether leaving correlated with an increase in space use overlap between troops. The monthly space use overlaps of each troop were also compared to the time spent outside the reserve each month, using Spearman rank correlations to assess whether the space use overlap with other troops increased during months when they spent more time outside the reserve.

The spatio-temporal shifts in the space use area of each troop were analysed by constructing matrices of month x month intra-troop space use overlap for all troops. Adjusted residuals of each troop's inter-monthly space use overlaps were calculated using Matman™

(De Vries *et al.*, 1993). The analyses generated adjusted residuals of Z values, with significance ($p \leq 0.05$) achieved at $Z > 1.96$ or < -1.96: with positive values indicating overlaps occurring more than by chance and negative values indicate overlaps occurring less than by chance. The percentage of possible combinations of monthly space use areas that were found to be significantly different (overlap less than by chance) indicate the amount each troop shifted its space use area over the year. Thus 100% would indicate that all monthly space use areas of a troop occupied significantly different areas from all other monthly space use areas; and 0% would indicate that no monthly space use areas of a troop occupied a significantly different area from any other space use area. The percentages of significantly different monthly space use areas for each troop were then compared to leaving category, using a Spearman's rank correlation to establish whether leaving correlated with an increase in the shifting of a troop's space use area.

The Friedman tests were performed using Instat. 3 (GraphPad Software, www.graphpad.com) and the Spearman rank correlations were performed using Statistica 7.1 (Statsoft Inc, www.statsoft.com).

2.5 Behaviour

2.5.1 Data collection

The behaviour of the baboons was recorded for one year from March 2006 to February 2007. During this time, eight days per month were spent in the reserve observing the baboons. The baboons were not observed outside the reserve. The troops were sampled opportunistically, by driving round the reserve until a troop was spotted. The road in the reserve follows a figure-of-eight one-way route, 66km long. I drove around the reserve at 40 km/h twice each day of sampling: once in the morning, starting half an hour after sunrise and once in the afternoon, starting four hours before sunset. To avoid sampling the areas along the beginning of the route before those along the end of the route every day, permission was gained from the reserve management to drive the wrong way around the route on weekdays. This was done for four days per month (or half of the sampling time). Individuals of troops were observed directly using 8 x 40 binoculars; observations were made from a car on the road. Although it is impossible to know the effects of the road and the car on the baboon troops, this was chosen as the least invasive and disruptive way to observe them, as cars are a very common sight in the reserve, and baboons would have been habituated to these. Scan sampling (Altmann, 1974) was used, with troops being scanned every minute for 40 minutes or until they moved out of sight. Although scan sampling may have under-estimated brief

behavioural events (like aggression) it was the only way to record all the behavioural categories in large, free living troops, which could move in and out of sight. Scanning every minute was used in order to get a better estimate of rarely occurring behaviours. All individuals were included in the scan (males, females and juveniles).

The following behavioural categories were scored: aggression, socio-positive behaviour, motor play, self-grooming, vigilance, foraging and mating. Aggression was scored when one baboon chased, bit, hit or roughly pulled another. Socio-positive behaviour was scored when baboons groomed each other or when one or more baboons engaged in play-fighting or chasing. Social play could be distinguished from aggressive interactions by the lack of screams from the participants and the lack of spectator interest from the rest of the troop. Play-fights also tended to be less one-sided than real fights (pers. obs.). Motor play was scored when a baboon ran to and fro' for no apparent reason, rather than running away from danger or to food or to keep up with the troop. Object play, when a baboon handled an object for no apparent reason, was only observed twice and was therefore included with motor play. Self-grooming was scored when a baboon teased through its own fur. Vigilance was scored when a baboon stood on its hind legs and scanned its surroundings, rather than just standing up to see what a nearby baboon was doing or to watch a fight in progress. Foraging was scored when a baboon was actively extracting food from the environment (e.g. digging food up or pulling food off trees), putting food in its mouth or chewing. Mating was scored whenever a male mounted a female.

Each time that the troop was scanned, the number of individuals involved in each of the above behaviours was recorded. As instantaneous scanning was used, no baboon was assigned more than one behaviour for the same minute, though baboons not performing any of the above mentioned behaviours (e.g. just sitting or moving) were not assigned behaviours.

For each troop sampled, I also recorded an estimate of the average number of individuals visible for each group scan during the sample, together with the direction of movement of the troop, the GPS co-ordinates of the location and the time and date of the sample.

To identify the troop under observation in each sample, the time, GPS co-ordinates and the direction of troop movement were matched up against the information on troop movement from the data obtained from the cell-phone telemetry collars. Only on two occasions was a troop observed twice in one day: AS39 on 20/08/2006 at 8:45 am and at 3:25 pm; and AS41 on 11/06/2006 at 9:14 am and at 3:02 pm.

2.5.2 Data analysis

For each troop, to obtain the total proportion of time spent performing each behaviour, the total frequency (number of occurrences) of each behaviour over all samples was divided by the total number of 'baboon minutes' for which the troop was observed over all samples, using the following formula:

$$P = F / Bm \qquad [Bm = (m_1 \times n_1) + (m_2 \times n_2) + (m_3 \times n_3)....]$$

where:

P is the total proportion of the time spent performing a behaviour by the baboons in a troop;

F is the total frequency of the behaviour over all samples for the troop (i.e. over all observation sessions);

Bm is the total number of baboon minutes for which the troop was observed over all observation sessions;

m is the duration of one observation session in minutes (m_1 = duration of session 1; m_2 = duration of session 2 etc.); and n is the average number of baboons visible during each group scan for each session (n_1 = average number of baboons in sample 1; n_2 = average number of baboons in sample 2 etc.).

The number of baboon minutes in a sample was calculated by multiplying the number of minutes in the observation session (equal to the number of times the troop was scanned) by the average number of baboons visible during each group scan. The baboon minutes for each session were added together to obtain the total number of baboon minutes for which each troop was observed. 'Baboon minutes' is essentially the total number of behavioural observations possible for each troop during the study, and is therefore the best indicator of sampling effort across the troops.

These calculations provided the proportion of the total time for which each troop was observed in which the baboons spent performing a behaviour of interest, with P = 1 indicating that all the baboons in the troop were constantly performing the behaviour and P = 0 indicating that the behaviour was not performed at all.

The GPS data from the troops were used to give each troop a status (non-leaver, leaver or occasional leaver) based on the amount of time it spent outside the reserve. The proportion behavioural data were arcsine transformed and a multivariate analysis of variance (MANOVA) was used to test if troop status (leavers, occasional leavers and non-leavers) influenced behaviour, with the number of baboon minutes for which a troop was observed included as a covariate. A MANOVA was used since the behaviours scored were not

independent. Tukey *post hoc* tests were used to identify which behaviours were contributing to the differences between troops of different status when $\alpha \leq 0.05$. Analyses were performed using Statistica 7.1 (Statsoft Inc, www.statsoft.com).

2.6 Information from farmers

2.6.1 Data collection

Questionnaire surveys were used to obtain information from farmers about patterns in raiding behaviour and their responses to baboon raiding. The questionnaire was composed jointly by myself and Johnny Hennop of the Suikerbosrand management, and included questions useful to my study and questions of interest to the Suikerbosrand (Figure 3). English and Afrikaans versions were sent to all of the 25 landowners within the Suikerbosrand area.

2.6.2. Data analysis

Those questions with choices for answers (e.g. Question 6; Figure 3) where each respondent chose only one option were analyzed using chi square tests, to analyse the likelihood of some responses occurring more often than chance.

The rest of the responses in the questionnaire were analysed qualitatively.

Questionnaire on Baboon activity:

(Please answer the questions below and post back in supplied envelope.)

1). What do you farm?
2). What size is your farm (in hectares)?
3). How much of your land is actually cultivated (in hectares)?
4). Do baboons ever raid your farm?
Yes: ☐ No: ☐
5). During which months do baboons most often raid your farm?
6). How often do raids occur during peak times?
Daily: ☐ Every other day: ☐ Twice a week: ☐ Once a week: ☐
Less than once a week: ☐
7). When, during the day, do baboons usually raid your farm?
Morning: ☐ Mid-day: ☐ Afternoon: ☐ Night: ☐
8). Is damage caused by solitary animals or do troops work together when raiding?
Solitary animals: ☐ Troops: ☐
9). Approximately what areas worth of crops do you lose to baboons every year (in hectares)?
10). What other damages except for crop raids do baboons cause through their raids e.g. fruit trees, poultry, damages to infrastructure etc?
11). What are your estimated Financial losses due to baboon raids every year (in rands)?
12). Have any of the baboons on your property been noticed as being marked with collars?
Yes: ☐ No: ☐
13). Have any baboons acted in a threatening manner towards family members or employees and if so what were the circumstances?
Yes: ☐ No: ☐
If yes, please explain:
14). Do you ever shoot baboons? If so, About how many baboons do you shoot every year?
None: ☐ 1 – 5: ☐ 6 – 10: ☐ 10 – 15: ☐ 15 – 20: ☐
20 – 30:☐ 30 – 40: ☐ more than 40: ☐
15). Which baboons do you usually target?
Big males: ☐ Big females: ☐ Small males: ☐
Small females: ☐ Infants: ☐ random individuals: ☐
16). Does shooting baboons seem effective as a way of reducing amount they raid?
Not at all effective: ☐ Somewhat effective: ☐ Very effective: ☐
17). Have you tried anything else to stop baboons raiding your farm? If so, what?
Nothing: ☐ Electric fences: ☐ Scarecrows: ☐ Dogs: ☐ Other: ☐
If other, please explain:
18). How affective have these methods been?
Not at all effective: ☐ Somewhat effective: ☐ Very effective: ☐
19). What is your opinion on the roll Nature Conservation should play in managing the baboon population?

All answers are kept confidential.

The answering of this questionnaire will assist us in compiling and implementing a "management plan" that will work towards the conservation of the ecosystem and manage the effects that Baboons might have.

Figure 3 Questionnaire survey sent to farmers around the Suikerbosrand Nature Reserve.

Chapter 3: Results

3.1 GPS data

Of the 12 known troops in the Suikerbosrand Nature Reserve at the time of study, an adult female in 11 troops was successfully collared. Of these 11, one collar malfunctioned and another only worked for the second half of the study period (i.e. from September 2006). Therefore, GPS data were available for 9 of the 12 troops from March 2006 to February 2007 and for a 10th troop from September 2006 to February 2007.

The home ranges of the troops taken over the entire year varied from 15.7 km^2 to 55.6 km^2. However, monthly space use areas were much smaller, varying from 2.1 km^2 to 28 km^2. This difference is due to the troops shifting their space use areas temporally and spatially. There was a wide range in within-troop variation in space use area, with overlap between a troop's space use area for one month compared to the same troop's space use area for a different month ranging from 0% to 100%. Inter-troop overlap was also very variable with some troops only overlapping a few percent with one or two other collared troops for a few months of the year, and other troops sharing most of their space use area with several other troops for most of the year. The troops also varied in the amount of time spent outside the reserve, with some troops never leaving the reserve and others spending most of their time on privately owned land.

Figure 4 shows the extent of each troop's home range, taken over the entire year in order to display the general location of each troop. The troops' names (e.g. AS55) used below were obtained from the names of the cell phone telemetry collars used to track them. Although many troops were moving out onto farmland to the east, south and west of the reserve, the new land in the north of the reserve was still largely unoccupied.

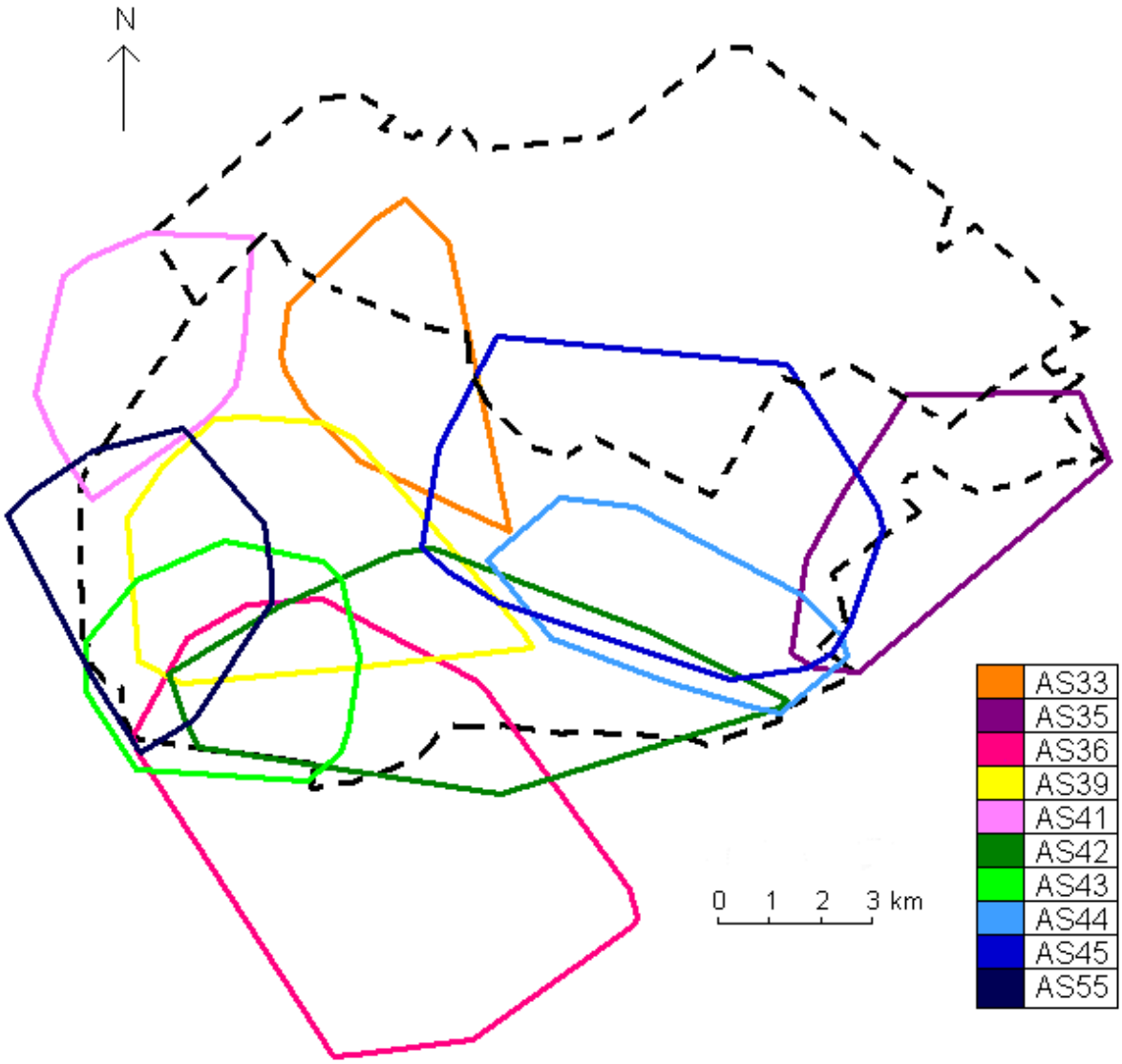


Figure 4 Map of the Suikerbosrand Nature Reserve showing minimum area convex polygons constructed around all GPS data points throughout the year (March 2006 to February 2007) for each of the 10 troops successfully monitored with GPS collars. AS33: orange; AS35: purple; AS36: dark pink; AS39: yellow; AS41: light pink; AS42: dark green; AS43: light green; AS44: light blue; AS45: blue; AS55: navy blue. Data for AS44 were only available for 6 months, from September 2006 to February 2007, and no data were available for AS40 as this collar malfunctioned. The reserve boundary and the fence separating the new land are shown in stippled black.

3.1.1 Time spent outside the reserve

Of the 10 troops for which GPS data were available, two of the troops never left the reserve, five troops spent less than 5% of their time outside the reserve, and three troops spent more than 40% of their time outside the reserve (Table 1). Based on these differences, troops

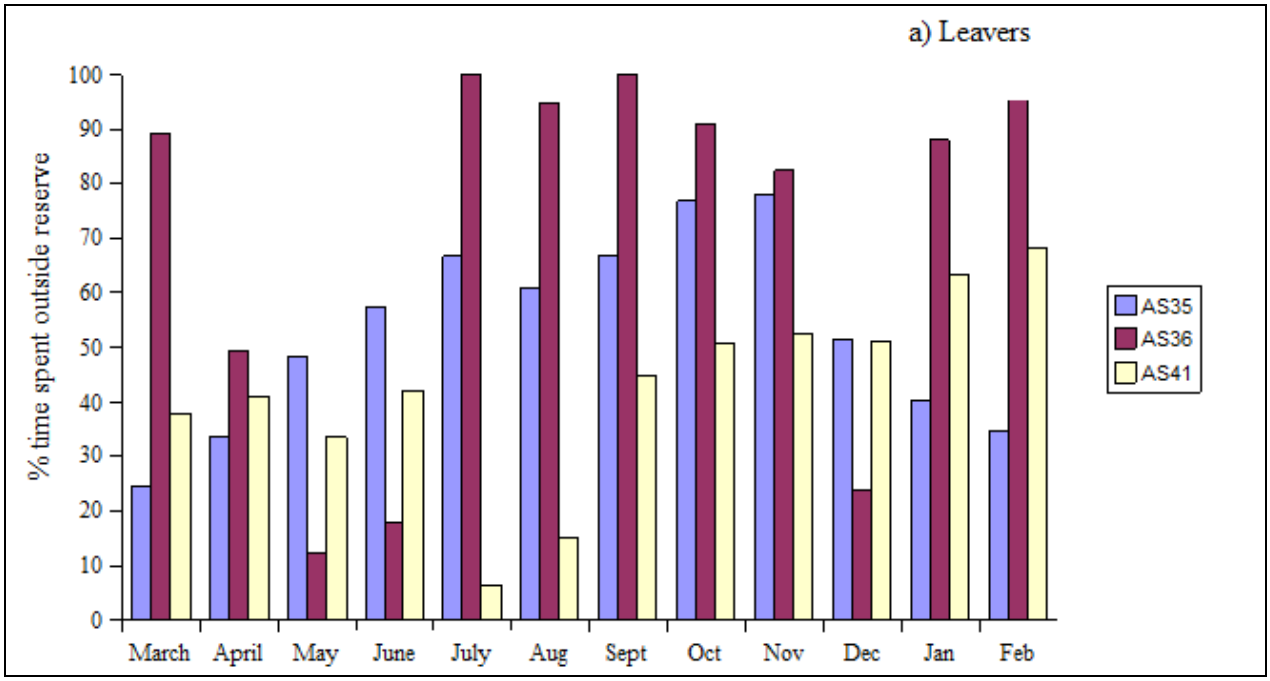
were assigned to one of three categories: leavers (L) - spent more than 40% of their time outside the reserve; occasional leavers (O) - spent between 0 and 5% of their time outside the reserve; and non-leavers (N) - never left the reserve during the study (Table 1). The amount of time spent outside the reserve, however, did not necessarily correlate with time spent raiding farmland so leaver troops did not necessarily spend more time raiding farmland than occasional leaver troops.

Table 1 Percentage of time spent outside of the reserve by 10 baboon troops in Suikerbosrand Nature Reserve (March 2006 – February 2007). The status of a troop was based on the percentage of time spent outside the reserve.

Troop identity	% time outside the reserve	Status
AS33	0.0	Non leaver
AS35	52.7	Leaver
AS36	74.1	Leaver
AS39	0.0	Non leaver
AS41	46.4	Leaver
AS42	3.3	Occasional leaver
AS43	4.3	Occasional leaver
AS44*	2.3	Occasional leaver
AS45	2.3	Occasional leaver
AS55	3.8	Occasional leaver

* Data for AS44 were available for only 6 months from September 2006

I predicted that troops leaving the reserve to raid farmland would spend more time outside the reserve in the early dry season when maize ripens, and troops leaving the reserve to forage on natural land would spend more time outside the reserve during the late dry season, when food was scarce in the reserve. Although the seasonality of time spent outside the reserve varied widely between troops (Figure 5a, b), the Friedman test revealed a significant effect of month on the time spent outside for occasional leavers ($Fr = 24.43$; $p = 0.011$; $n = 4$) with the most time being spent outside in June, July, August, January and February. (AS44 was omitted from analysis.) There was no significant effect of month on time spent outside the reserve for leavers ($Fr = 12.47$; $p = 0.330$, $n = 3$).



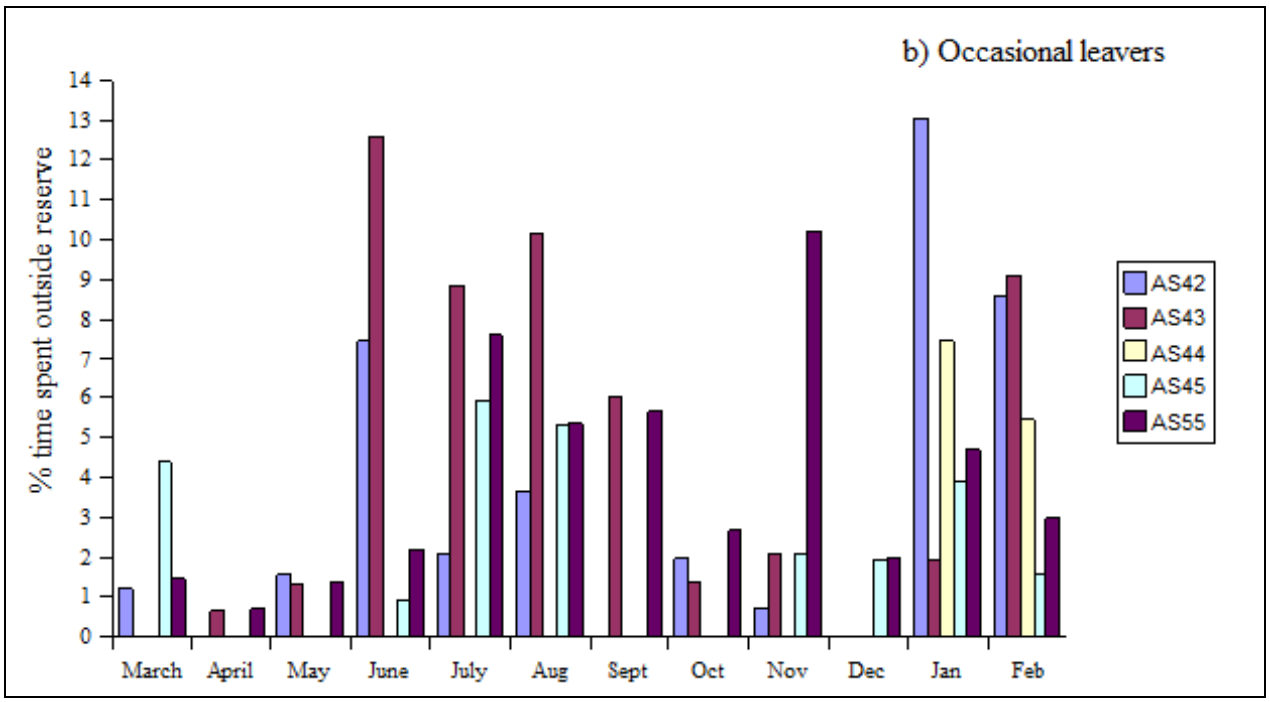


Figure 5 Percentage time spent outside the reserve by a) leavers and b) occasional leavers for each month from March 2006 to February 2007. Data for AS44 were available from September 2006 only.

3.1.2 Troop size

The number of baboons counted in each troop throughout the 2006 census ranged from 16 to 62. These values are likely to be an underestimation of troop size (the sum of the counts is only 443, whereas the Suikerbosrand management had estimated the total population in the reserve at 771 baboons). However, these values provide an idea of the relative sizes of the troops (Figure 6). I predicted that troops that leave the reserve, especially if raiding farmland, would be larger than troops that do not leave the reserve. However, the Spearman rank correlation indicated no relationship between troop size and leaving status ($r = -0.09$; $p = 0.811$).

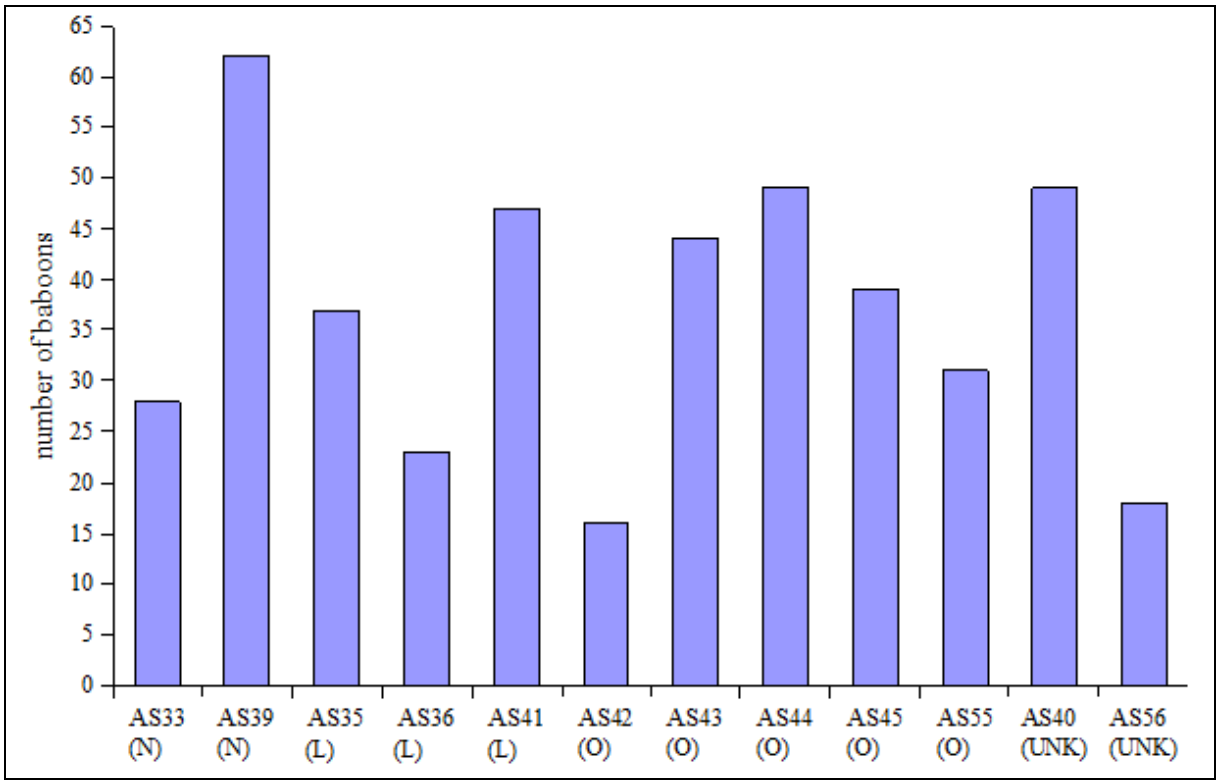


Figure 6 The number of baboons counted in 12 baboon troops in the Suikerbosrand Nature Reserve during the census in 2006.

The data for two troops that were not successfully collared, AS40 and AS56 (this name comes from the collar intended for the troop) have been included for comparison. N = non-leaver; L = leaver; O = occasional leaver.

3.1.3 Space use area

As some of the troops shifted their space use areas substantially throughout the study period, the home ranges as calculated for the whole year of sampling were larger than the actual space used by the troops from day to day (Figure 7). Therefore, mean monthly space use areas have been provided instead (Figure 8). I predicted that troops leaving the reserve to raid farmland would have small monthly space use areas and troops leaving the reserve to forage on fallow land would have large monthly space use areas. However, the Spearman rank correlation indicated no relationship between mean monthly space use area and leaving status ($r = 0.165$; $p = 0.657$).

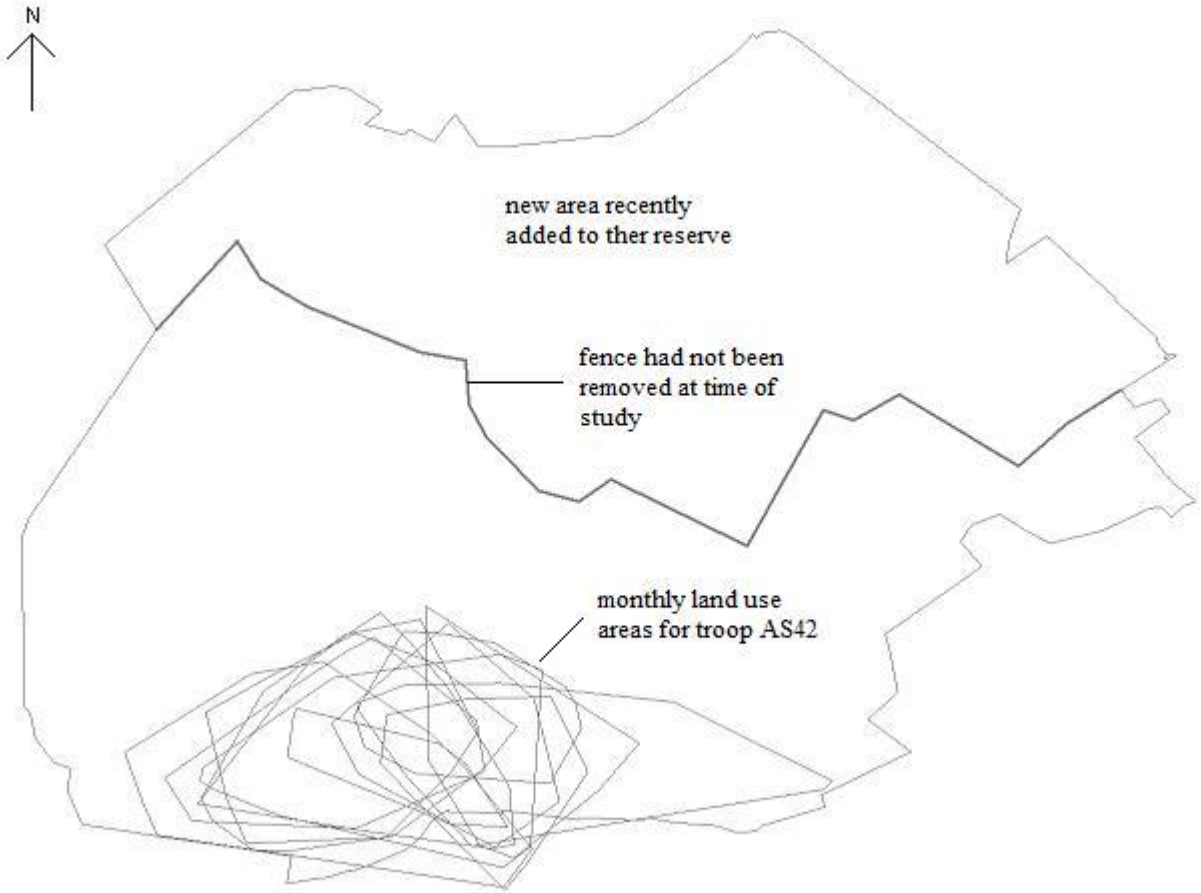


Figure 7 Representative map of the monthly space use of troop AS42, an occasional leaver troop. For troops such as this that shifted their areas of land use to a high degree throughout the year, a home range taken over the whole year would considerably overestimate the area utilized by the troop.

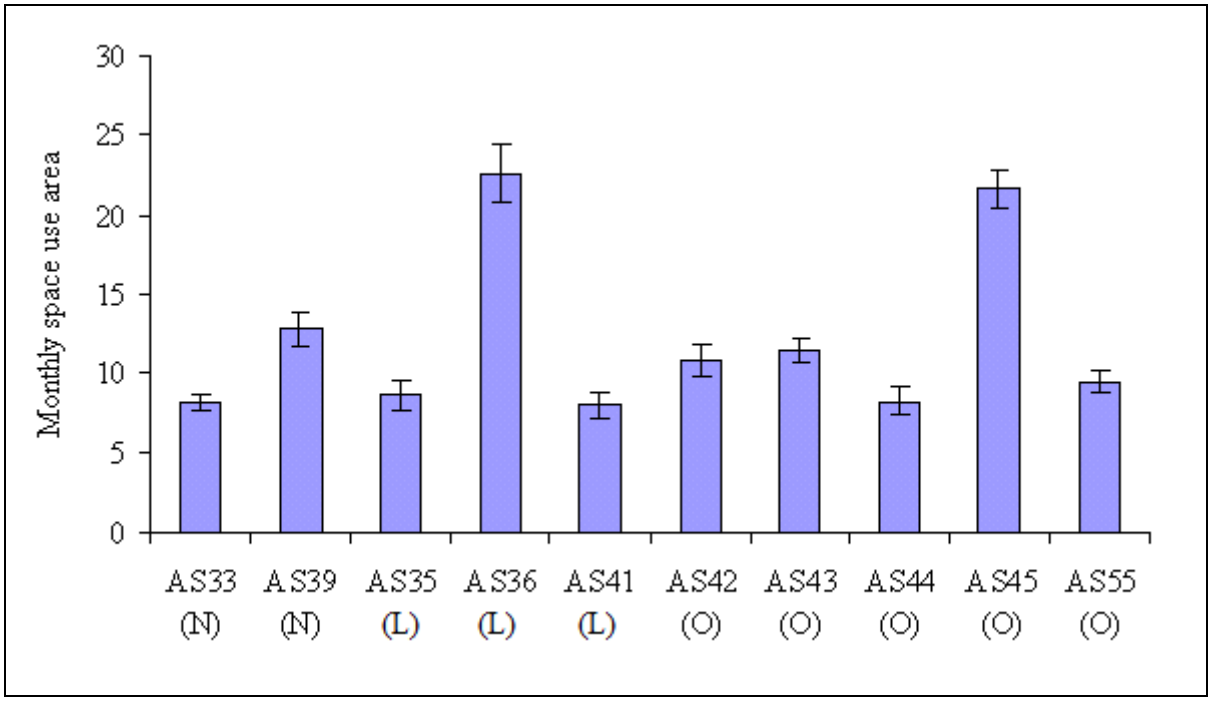


Figure 8 Mean (with standard error bars) monthly space use areas (km^2) for 10 baboon troops in the Suikerbosrand Nature Reserve. N = non-leaver; L = leaver; O = occasional leaver.

3.1.4 Monthly space use overlap

Inter-troop space use overlap was very variable with some troops only overlapping a few percent with one or two other troops for a few months of the year, and other troops sharing most of their space use areas with several other troops for most of the year (Table 2; Figure 9). I predicted that troops leaving the reserve to raid farmland would have large space use overlaps with other troops and troops leaving the reserve to forage on uncultivated land should have small space use overlaps with other troops. The Spearman rank correlation did show a significant correlation between space use overlap and leaving status ($r = 0.651$; $p = 0.049$), with occasional leavers overlapping with other troops the most and leavers overlapping with other troops the least.

Table 2 The number of other troops that each troop overlapped with and total % space use overlap for each troop, from March 2006 To February 2007 in the Suikerbosrand Nature Reserve. Data for AS44 were only available from September 2006. N = non-leaver; L = leaver; O = occasional leaver.

Month	AS33 (N)		AS35 (L)		AS36 (L)		AS39 (N)		AS41 (L)		AS42 (O)		AS43 (O)		AS44 (O)		AS45 (O)		AS55 (O)	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
March	0	0	0	0	2	8	3	7	0	0	2	2	3	35			0	0	2	10
April	0	0	1	4	3	12	4	24	0	0	3	32	3	48			2	3	2	19
May	0	0	0	0	4	18	5	23	0	0	3	9	3	88			2	1	3	44
June	0	0	1	4	3	31	4	28	0	0	1	12	3	114			1	2	3	61
July	0	0	1	7	0	0	3	30	0	0	1	19	2	50			1	4	2	44
Aug	0	0	1	5	2	10	3	18	0	0	2	19	3	62			1	2	2	53
Sept	0	0	0	0	0	0	3	23	0	0	2	39	3	47	1	19	1	6	2	26
Oct	0	0	0	0	2	23	3	28	0	0	3	62	4	56	1	42	1	16	2	26
Nov	1	12	1	4	2	31	3	24	0	0	3	85	4	68	1	71	3	23	2	7
Dec	0	0	1	17	3	37	4	53	1	1	3	92	4	107	1	48	2	25	2	34
Jan	0	0	1	10	2	22	3	36	0	0	3	70	4	96	1	39	2	37	2	36
Feb	0	0	1	17	1	4	3	30	0	0	3	21	3	31	1	62	2	27	2	21

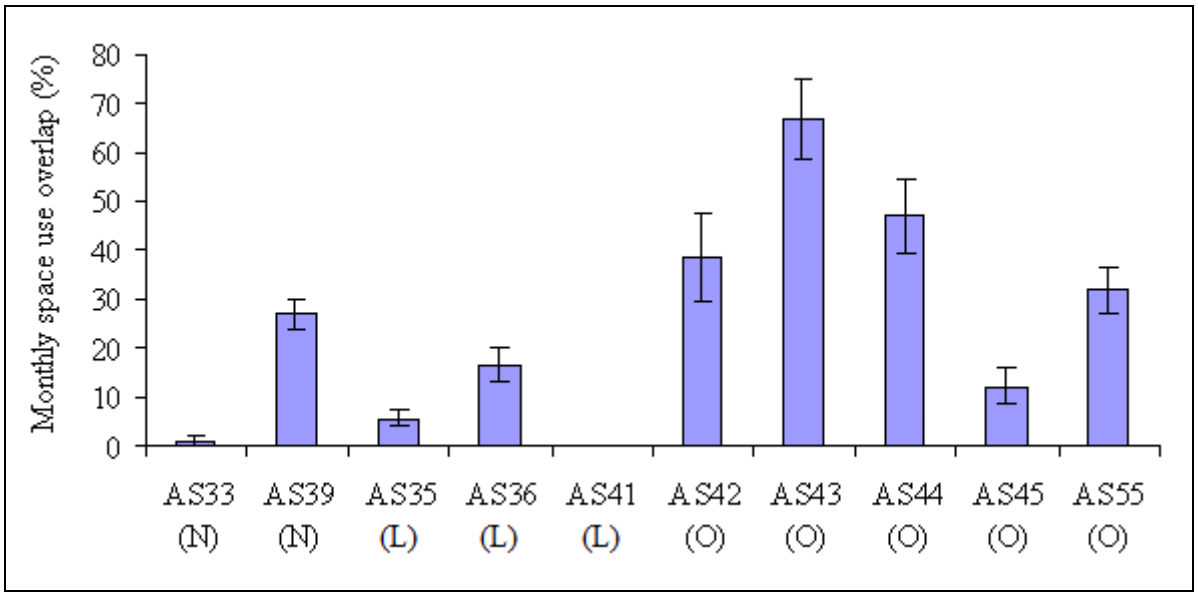


Figure 9 Mean (with standard error bars) monthly space use overlap with other troops for 10 baboon troops in the Suikerbosrand Nature Reserve. N = non-leaver; L = leaver; O = occasional leaver.

I predicted that troops leaving the reserve to forage on uncultivated land would have smaller space use overlaps with other troops at times of the year when they spent more time outside the reserve, while troops leaving the reserve to raid farmland would have larger space use overlaps at time of the year when they spent more time outside the reserve. Spearman rank correlations found no relationship between space use overlap and the percentage of time

spent outside the reserve for 9 of the 10 troops for which space use data were available. Only the leaver troop AS36 showed a significant (negative) relationship, overlapping with other troops less during months when it spent more time outside of the reserve (Table 3).

Table 3 Results of Spearman rank correlations comparing space use overlap and time spent outside the reserve for 10 baboon troops in the Suikerbosrand Nature Reserve. Significant relationships (Spearman rank correlation) are shown in bold. N = non-leaver; L = leaver; O = occasional leaver.

Troop name and leaving status	Monthly space use overlap (mean ± standard error)	% time outside reserve (mean ± standard error)	R value	p value
AS33 (N)	1.01 ± 1.01	0.00 ± 0.00	NA	NA
AS39 (N)	26.99 ± 3.13	0.00 ± 0.00	NA	NA
AS35 (L)	5.70 ± 1.77	53.28 ± 5.03	-0.28	0.385
AS36 (L)	**16.45 ± 3.65**	**70.67 ± 9.99**	**-0.62**	**0.033**
AS41 (L)	0.12 ± 0.12	42.26 ± 5.15	0.16	0.621
AS42 (O)	38.47 ± 8.94	3.36 ± 1.20	-0.05	0.887
AS43 (O)	66.79 ± 8.12	4.50 ± 1.31	0.01	0.966
AS44 (O)	46.85 ± 7.55	2.15 ± 1.38	0.08	0.874
AS45 (O)	12.19 ± 3.71	2.16 ± 0.63	0.00	0.996
AS55 (O)	31.84 ± 4.79	3.90 ± 0.83	-0.11	0.727

Note: there are no results for the non-leavers as they never left the reserve.

3.1.5 Space use shifts

Using the data from the matrices of adjusted residuals of space use overlap, I generated the percentage of possible combinations of monthly space use areas that occupied significantly different locations for each troop (Figure 10). In other word, Figure 10 indicates the amount each troop shifted its space use area over the year, with 100% indicating that all monthly space use areas of a troop occupied significantly different areas from all other monthly space use areas and 0% indicating that no monthly space use areas of a troop occupied a significantly different area from any other space use area (Figure 10). The matrices with the adjusted residuals for each troop for which data were available have been included as Appendix 1.

I predicted that troops that did not leave the reserve would shift their space use areas less than other troops throughout the year. However, the Spearman rank correlation found no

relationship between percentage of significantly different monthly space use areas and leaving status (r = 0.30; p = 0.387).

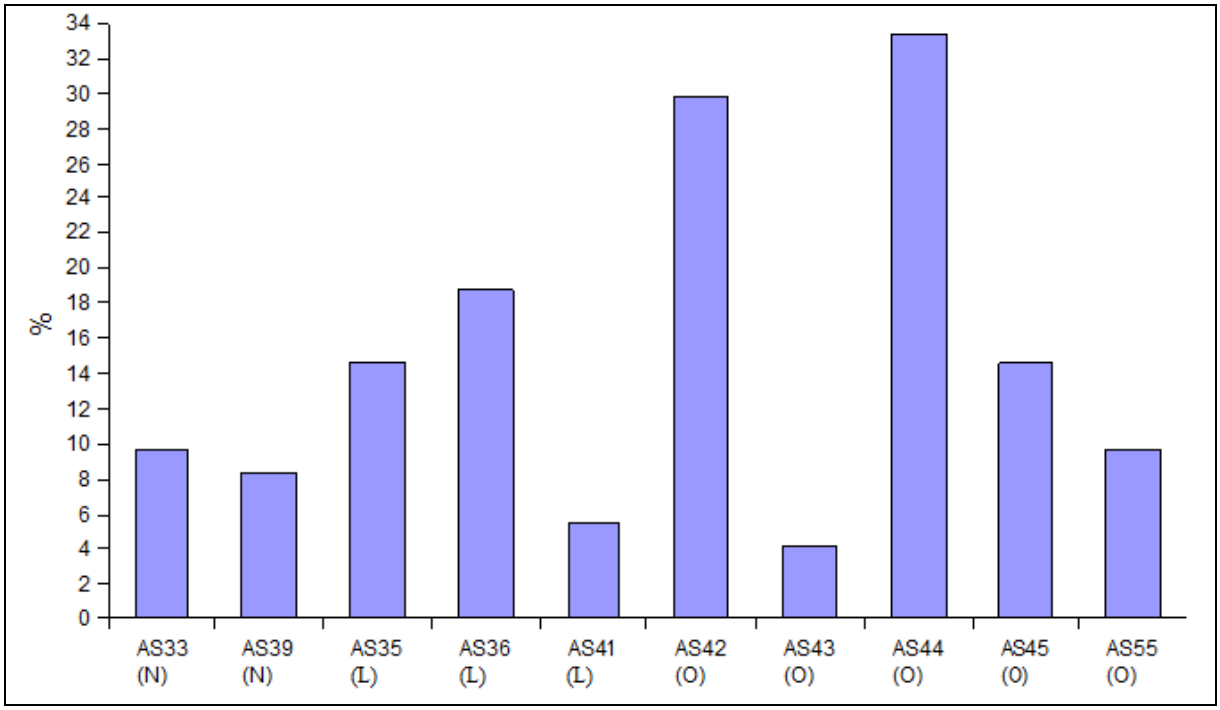


Figure 10 The percentage of possible combinations of monthly space use areas that are significantly different (Z > 1.96, p < 0.05) for 10 baboon troops in the Suikerbosrand Nature Reserve. N = non-leaver; L = leaver; O = occasional leaver.

3.2. Behaviour

Of the10 troops for which GPS data were available, one of the leaver troops (AS35) was not sampled, since its home range did not overlap with the road that I travelled in Suikerbosrand Nature Reserve during my study. Therefore, I analysed behavioural data for only 9 troops: 2 non-leavers, 2 leavers and 5 occasional leavers (Table 4). Most of the occasional leavers (AS42, AS43, AS44 and AS55) were only observed during the second half of the study period (September 2006 to February 2007) as their areas of space use only overlapped with the road during this period.

Table 4 The number of sampling sessions, baboon minutes and total minutes of observation time for each of 10 baboon troops in the Suikerbosrand Nature Reserve.

Troop Identity	Leaving Status	Number of Sampling Sessions	Baboon Minutes	Total Minutes
AS33	Non-leaver	11	1845	146
AS39	Non-leaver	21	4380	388
AS35	Leaver	0	0	0
AS36	Leaver	5	892	62
AS41	Leaver	22	4852	298
AS42	Occasional Leaver	13	2000	191
AS43	Occasional Leaver	2	390	26
AS44	Occasional Leaver	7	1100	81
AS45	Occasional Leaver	4	510	42
AS55	Occasional Leaver	1	150	10

Overall, foraging was the most common behaviour exhibited by the baboons, with troops spending around 15 to 40 % of their time foraging (Figure 11a). Socio-positive interactions were the second most common, accounting for around 5 to 10 % of the time (Figure 11a). Aggression was the third most common, accounting for around 1 to 3 % of the time and self-grooming, mating, vigilance and motor play were rarely seen, with each accounting for less than 1 % of the baboons' time (Figure 11b). Because there was such a large difference in the amount that different behaviours were observed, the data for foraging and socio-positive interactions (Figure 11a) has been displayed separately from the data for the other behaviours (Figure 11 b) so that inter-troop differences in rare behaviours can be seen.

The MANOVA revealed that the covariate, number of baboon minutes, had no significant effect on the behaviour data ($F_{1,5} = 130.46$; $p = 0.066$). The leaving status of the troops, however, did have a significant effect ($F_{2,10} = 56.21$ $p = 0.018$). *Post hoc* tests revealed that this significance was primarily due to the data on foraging and on self-grooming. Leavers displayed significantly more self-grooming than occasional leavers, with non-leavers falling somewhere in between. Non-leavers displayed significantly more foraging than leavers, with occasional leavers falling somewhere in between. Detailed comparisons of behaviours among the troops (i.e. the *post hoc* analyses) are provided below.

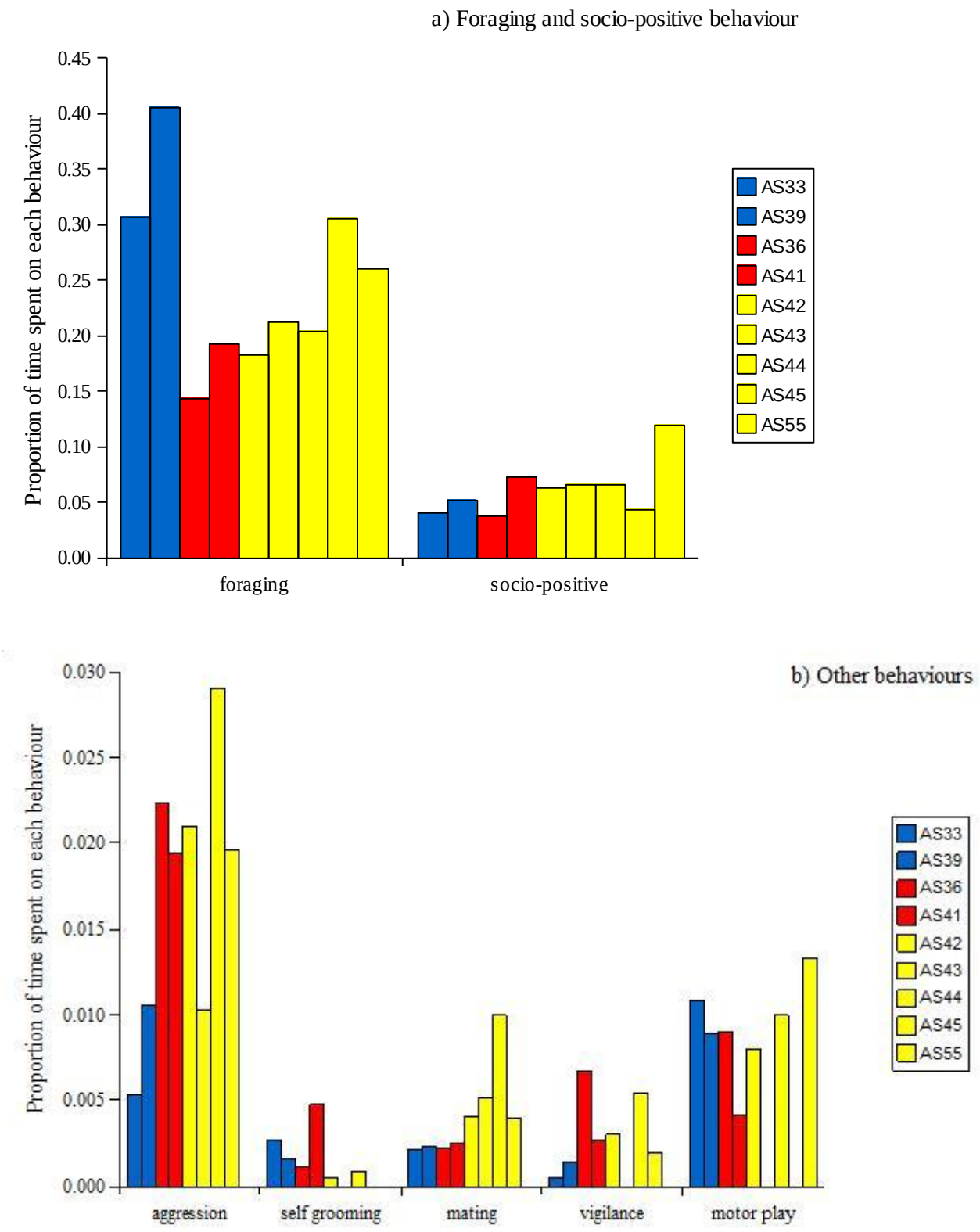


Figure 11 Total proportion of the time that each of 9 baboon troops spent on a) foraging and socio-positive behaviour and b) aggression, self-grooming, mating, vigilance and motor play. Data for non-leavers are shown in blue, leavers in red and occasional leavers in yellow.

3.2.1 Aggression, self-grooming and mating

Aggression, self-grooming and mating were all predicted to be more common in raiding troops than in non-raiding troops due to lethal retaliation from farmers. Although the levels of aggression observed for non-leavers were lower than those observed for the leavers and most of the occasional leavers (Figure 11a), the difference was not significant. The results therefore do not confirm this prediction. The two occasional leaver troops with low levels of observed aggression (AS43 and AS55), were only observed for 2 and 1 sampling sessions, or 390 and 150 baboon minutes, respectively (Table 4).

Self-grooming was significantly different between leaving categories. However, while leaver troops had high levels of self-grooming as predicted, occasional leavers had very low levels of self-grooming and non-leavers had levels of self-grooming close to those of the leavers (Figure 11b). The results therefore support the prediction for the leaver troops, but not for the occasional leaver or non-leaver troops.

Although the levels of mating observed for the occasional leavers (except for troop AS55) were higher than those observed for leavers and non-leavers (Figure 11b), there was no significant difference in levels of mating between troops in the three categories. The results therefore do not confirm this prediction. The occasional leaver troop with no observed mating (AS55) was only observed for 1 sampling session or 150 baboon minutes (Table 4).

3.2.2 Foraging

Foraging was predicted to be more common in non-raiding troops than in raiding troops due to intensive foraging outside the reserve by raiding troops. The results confirm this prediction, with non-leavers displaying significantly more foraging than leavers, and with occasional leavers falling somewhere in between (Figure 11a).

3.2.3 Vigilance, motor play and socio-positive behaviour

Vigilance, motor play and socio-positive behaviour were not predicted to differ between raiding and non-raiding troops. Although the levels of vigilance observed for non-leavers were lower than those observed for the leaver and most of the occasional leaver troops, the difference was not significant (Figure 11b). The two occasional leaver troops with low levels of observed vigilance (AS 43 and AS55), were only observed for 2 and 1 sampling sessions, or 390 and 150 baboon minutes, respectively (Table 4).

Although there was quite a large variation in the levels of motor play between troops (Figure 11b), there was no significant difference in levels of motor play between troops in the three leaving status categories.

There was no difference in levels of socio-positive behaviour between troops in the three categories (Figure 11a). Occasional leaver AS55, which displayed very high levels of socio-positive behaviour, was only observed for 1 sampling session or 150 baboon minutes (Table 4).

3.3 Questionnaire surveys

Of the 25 questionnaires distributed to land owners in the vicinity of the Suikerbosrand Nature Reserve, 14 (56%) were returned. Of the19 questions in the questionnaire, only 6 could be analysed using statistical tests (questions 4, 6, 13, 14, 16 and 18). These were the multiple choice questions for which respondents each chose only one answer. The rest were considered qualitatively.

For question 4 (Do baboons ever raid your farm?), a significant majority (11 of 14) of the respondents answered yes, indicating that most land owners in the area do get baboons on their land ($\chi_1^2 = 4.57$; $p = 0.033$).

For question 6 (How often do raids occur during peak times?), 4 of the respondents said daily, 2 said every other day, 1 said twice a week, 1 said once a week and 5 said less than once a week. There was no significant trend in the answers to this question ($\chi_4^2 = 3.62$; $p = 0.460$).

For question 13 (Have any baboons acted in a threatening manner towards family members or employees and if so what were the circumstances?), a significant majority (12 of 14) of the respondents answered no, indicating that the baboons do not pose a threat to people ($\chi_1^2 = 7.14$; $p = 0.008$). Of the 2 that answered yes, 1 said only that his workers are scared of the baboons and refused to go near them, while the other said that the baboons come close to his house in a threatening way.

For question 14 (Do you ever shoot baboons? If so, about how many do baboons do you shoot every year?), a significant majority (10 of 14) of the respondents answered none ($\chi_7^2 = 48.86$; $p = 0.000$). Of the remaining 4 respondents, 3 answered between 1- 5 baboons per year and one answered between 10 - 15 baboons per year.

For question 16 (Does shooting baboons seem effective as a way of reducing the amount they raid?), 5 of the 7 respondents who answered the question answered somewhat effective and the other two answered not at all effective. There was no significant trend in the

answers to this question ($\chi_2^2 = 5.43$; $p = 0.066$). Two of the respondents who claimed not to shoot baboons answered this question as well, indicating inconsistency in the responses. Their answers have been included here. One answered 'not at all effective' while the other answered 'somewhat effective'.

For question 18 (How effective have these methods [alternatives to shooting] been?), 2 of the respondents who answered this question chose not at all effective, 5 chose somewhat effective and 2 chose very effective. There was no significant trend in the answers to this question ($\chi_2^2 = 2$; $p > 0.368$). The alternate methods in question were electric fencing, dogs, scarecrows and scaring baboons with loud noise and bright light.

3.3.1 Raiding by baboons

Most land owners reported that baboons do raid their farms, though losses tended to be minimal (Table 5). Only maize and bean farmers sustained significant losses (numbers 3 & 10), though one maize farmer reported losing only garden fruit and eggs (number 14) and one dairy farmer had milk machines broken by baboons (number 8). The maize and bean farms (numbers 3 & 10) were raided daily, while most other plots were raided less often. Several plots were raided mainly during winter for items such as garden fruit and vegetables (numbers 1, 4 & 14), garbage (number 6), animal fodder (number 7) and eggs (number 14). Others were raided more throughout the year for items such as maize and beans (number 3) and water (number 13). Others reported increased raiding when crops or fruit were ripe (numbers 5, 9 & 10). Garden fruit and vegetables and fodder were also reported by two land owners to be raided mainly during the summer months (numbers 11 & 12). Overall, raiding was reported throughout the year, with an increase in peak raiding reported during winter (Figure 12).

Table 5 Summary of answers to questions relating to farmer's losses caused by baboons in the vicinity of Suikerbosrand Nature Reserve.

Respondent number	items farmed	raiding reported	items raided	which months most raiding	frequency of raiding	area of crops lost (ha)	finacial losses per year in R
1	sheep, cattle	yes	garden fruit & veg	winter, end summer	daily	0	mimimal (recently)
2	nothing	no	nothing	winter	less than once a week	0	0
3	maize, beans	yes	corn, beans	all year	daily	25 out of 200	40 000
4	nothing	yes	garden fruit & veg	winter, spring	daily	0	unknown
5	nothing	yes	garden fruit & veg	when corn is ripe	less than once a week	0	very small
6	poultry	yes	dustbins	June to September	less than once a week	0	0
7	sheep, cattle	no	sheep's fodder	July to August	less than once a week	0	only slight
8	cattle	yes	nothing	right through the year	NA	0	12 000 (milk machines)
9	nothing	yes	garden fruit	fruit time	once a week	0	0
10	maize, beans, cattle	yes	corn, beans	Jan to March and near harvest	daily	8 out of 540 (last year)	56 000 (year befor last)
11	cattle, fruit, veg	yes	fruit & veg	Aug to Dec	every other day	unknown	unknown
12	cattle	yes	garden fruit & eggs, cattle fodder	Nov to July	every other day	0	mimimal
13	nothing	no	water	all year	once or twice a week	0	0
14	cattle, maize, teff	yes	garden fruit & eggs	winter	less than once a week	0	0

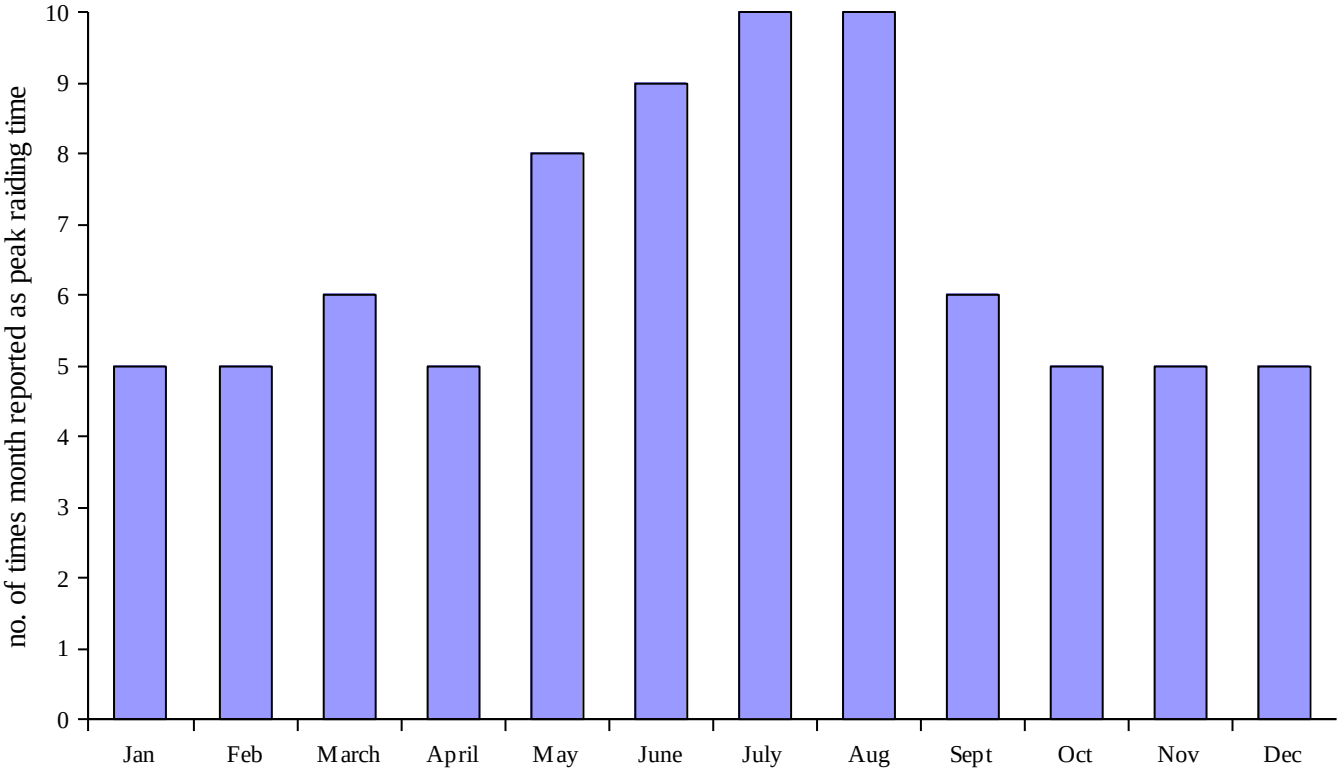


Figure 12 Number of times that raiding was reported in each month by farmers in the vicinity of Suikerbosrand Nature Reserve. The data were in response to Question 5 (During which months do baboons most often raid your farm?).

3.3.2 Reactions of farmers

Only four of the respondents reported shooting baboons. Others tried a variety of alternative strategies to reduce raiding such as using guard dogs, electric fences, scarecrows or using light and noise to scare away the baboons (Table 6). Both of the respondents who said that the baboons were acting threateningly towards people reported shooting baboons (numbers 3 & 5). Both of the farmers who were regularly suffering financial losses reported shooting baboons (numbers 3 & 10). The only other person to report shooting baboons also mentioned that six of his dogs were killed by baboons (number 11). Of the four who shot baboons, three reported targeting large males (numbers 3, 5 & 11), one reported shooting large females (number 3) and two reported shooting individuals randomly (numbers 3 & 10). Shooting baboons was mostly reported as a partly effective way of reducing raiding, with one farmer claiming that the baboon troop would stay away from his farm for a day to a week after he shot one (number 10).

Four respondents reported using electric fencing to keep baboons out (numbers 1, 2, 3 & 6). They found this method to be anything from very effective to not at all effective. Seven

respondents reported using dogs to keep baboons away (numbers 1, 2, 4, 8, 9, 12 & 13). Again, this was found to be anything from not at all effective to very effective, but mostly partially effective. Also, four of the respondents reported having dogs attacked or killed by baboons (numbers 6, 8, 9 & 11). Two respondents reported using light reflected from a mirror and / or loud noises such as fire crackers to scare away baboons (numbers 11 & 14). This was found to be somewhat effective. Finally, one respondent (number 9) reported using a scarecrow to keep baboons away. This was not at all effective.

Table 6 Summary of answers to questions relating to farmers' reactions to raiding by baboons in Suikerbosrand Nature Reserve.

no.	finacial losses per year in R	seen as threat	no. shot	target	effective	what else tried	effective	notes
1	mimimal (recently)	no	0	NA	NA	electic fencing, dogs	very	
2	0	no	0	random	somewhat	electic fencing, dogs	somewhat	
3	40 000	yes (scare workers)	10 to 15	big males, big females, random	not at all	electic fencing	not at all	
4	unknown	no	0	NA	NA	dogs	somewhat	
5	very small	yes (come near house)	1 to 5	big males	somewhat	nothing	NA	
6	0	no	0	NA	NA	electric fencing	very	dog savaged
7	only slight	no	0	NA	NA	nothing	NA	
8	12 000	no	0	NA	NA	dogs	NA	dogs killed
9	0	no	0	NA	NA	scarecrows, dogs	not at all	dogs killed
10	56 000 (prev. year)	no	1 to 5	random	somewhat	nothing	NA	stay away for a day or week when shot
11	unknown	no	1 to 5	big males	somewhat	noise	somewhat	6 dogs killed
12	mimimal	no	0	NA	somewhat	dogs	NA	
13	0	no	0	NA	NA	dogs	somewhat	
14	0	no	0	NA	NA	noise & mirror	somewhat	

Chapter 4: Discussion and Recommendations

4.1 Space use and raiding

4.1.1 Recap of Aims and Predictions

The primary aim of the space use aspect of this study was to use the GPS data to investigate which troops were raiding farmland and to investigate which troops, if any, are leaving the reserve due to resource scarcity. The data were also used to examine the behaviour of leaving and non-leaving troops. Time spent outside the reserve was taken as a general indication of the opportunity to raid farmland, and as either an indication of actual raiding or the need to forage outside of the reserve due to resource scarcity within the reserve.

Troops leaving the reserve to raid were expected to display the following characteristics: spending more time outside the reserve in the early dry season when maize is ripe, forming larger troops, using smaller areas of land on a monthly basis and / or overlapping more with other troops (especially at times of the year when they spend more time outside the reserve) and shifting their space use areas to a large extent throughout the year.

Troops leaving the reserve to forage on fallow land were expected to display the following characteristics: spending more time outside the reserve in the late dry season when resources are most scarce, forming larger troops (though not as large as raiding troops), using larger areas of land on a monthly basis and /or overlapping less with other troops (especially at times of the year when they spend more time outside the reserve) and shifting their space use areas to a large extent throughout the year.

Non-raiding troops that were able to find sufficient food within the reserve were expected to display the following characteristics: never leaving the reserve, forming smaller troops, using intermediate sized areas of land on a monthly basis and overlapping with other troops to an intermediate degree (intermediate meaning between that of raiding troops and troops foraging on fallow land) and shifting their space use areas to a small extent throughout the year.

4.1.2 Time outside the reserve

In terms of time spent outside the reserve, the 10 troops for which GPS data were available grouped naturally into 3 distinct categories. 2 troops (classified as non-leavers) never left the reserve, 5 troops (classified as occasional leavers) spent < 5 % of their time

outside the reserve and 3 troops (classified as leavers) spent between 45 and 75 % of their time outside the reserve.

The non-leaver troops are therefore likely to be troops that did not raid and are able to find enough food within the reserve. The other two categories of troops that did leave the reserve are likely to be troops that either raid farmland or forage on fallow land due to difficulty in finding sufficient resources within the reserve (or a combination of both of these). The occasional leaver troops were the most likely candidates for troops that were leaving the reserve specifically to raid farmland, as it is unlikely that troops would be able to sufficiently supplement their diet to any significant extent by foraging on fallow land for <5 % of the time. Cultivated land, however, could provide large quantities of food in very short periods of time.

The leaver troops were the most likely candidates for troops that are foraging on fallow land. As troops should not spend more time in the relatively high risk areas outside the reserve than necessary, the large amount of time spent outside the reserve by leaver troops suggests a foraging behaviour less efficient than the raiding of agricultural land. This does not mean, however, that the leaver troops are not raiding farmland in addition to foraging on fallow land.

These assumptions are supported by the findings of Segal (2008) who studied the diet of the same troops over the same period as this study. She found that the faecal matter of the two non-leaver troops averaged 0 and < 1 % maize over the year. The faecal matter of 4 of the 5 occasional leaver troops contained between 1 and 5 % maize, while that of the 5th occasional leaver troop (AS42) contained almost 25 % maize. Of the 3 leaver troops, sufficient faecal matter for analysis could only be gathered from 1 (AS41) which contained about 3 % maize. This pattern also fits the findings of Cowlishaw (1997 a & b) that baboons will avoid high risk areas if possible, and will forage on resource rich, high risk areas as quickly as possible before leaving for safer areas.

The division of the Suikerbosrand troops into the 3 categories is similar to the finding of Strum (1994) who found that olive baboon troops responded to a shortage of natural foraging land in a variety of ways, from enlarging or shifting home ranges or reducing troop sizes to avoid raiding, to raiding as a backup strategy or raiding as the primary foraging strategy.

In terms of the seasonality of time spent outside the reserve, the occasional leavers spent more time outside the reserve in the mid to late dry season and in the late rainy season than at other times of the year. This is contrary to the expectation that occasional leavers

would spend more time outside the reserve in the early dry season when maize is ripe. However, Segal (2008) found kernels of maize in the faecal matter of the troops throughout the year, indicating that farmers do not securely store their grain after the harvest, making it available long after the early dry season. It has also been found that baboons will feed on parts of the maize plant throughout its life cycle, not only on the fruit (Naughton-Treves et al., 1998). The increase in time spent outside during the late dry season may indicate that raiding behaviour is being stimulated be periods of natural food scarcity, as has been found by Naughton-Treves et al. (1998). Another possibility is that the abundant availability of maize in the early dry season allows troops to raid more efficiently, thus requiring less time out of the reserve during this part of the year.

There was no pattern to the seasonality of time spent outside the reserve by leaver troops. This suggests that leaver troops are responding to the availability of agricultural food and to natural food shortages in different ways, preventing a common pattern from emerging across all leaver troops.

4.1.3 Troop size

There was no relationship between troop size and leaving status. This is contrary to research suggesting that baboons form larger troops in response to greater predation pressure (Barton et al., 1996; Henzi et al., 1997). This could be because the normal predator defence of mobbing potential predators is unlikely to be effective against farmers with guns. Shooting of baboons by farmers may also be limiting the growth of troops that raid farmland.

4.1.4 Monthly space use area and monthly space use overlap

Based on the tendency towards correlation between home range size and resource availability (Barton et al., 1992), it was expected that troops that were raiding farmland would need less space than those that were not, and that those troops that were foraging on fallow land would use more space than those that were not. There was no relationship between leaving status and monthly space use area. However, there was a relationship between leaving status and monthly inter-troop overlap, with occasional leavers overlapping with other troops the most and leavers overlapping with other troops the least. This supports the idea that occasional leavers are primarily leaving the reserve to raid farmland, allowing them to overlap with other troops to a large extent, while leavers are primarily leaving the reserve to forage on fallow land and taking advantage of the lower density of baboons outside the reserve by overlapping less with other troops.

I also predicted that the trend toward greater or smaller space use overlaps would increase at times of the year when troops spent more time outside the reserve. There was, however, only a relationship for leaver troop AS36, which showed a significant (negative) relationship, overlapping with other troops less during months when it spent more time outside of the reserve. This supports the idea that this troop may be benefiting from leaving the reserve by decreasing its space use overlap with other troops. Why similar relationships were not found with other troops is unclear, although the difference in time spent outside the reserve at different times of the year for occasional leavers is so small as to make any significant relationship unlikely.

4.1.5 Space use shifts

It was predicted that troops that did not leave the reserve would shift their space use areas less than other troops throughout the year. However, there was no relationship between the extent to which troops shifted their space use areas throughout the year and leaving status. As there was no seasonal pattern to the time spent outside by leaver troops, it follows that they would not necessarily need to shift their home ranges to a large extent throughout the year. Also, the seasonal changes in time spent outside the reserve for occasional leavers were so small that they too would not have necessarily needed to shift their home ranges to a large extent.

4.1.6 Conclusions

The space use data suggest that the occasional leavers are leaving the reserve primarily to raid farmland and are likely to be responsible for the majority of raiding taking place; and the leavers are leaving the reserve primarily to forage on fallow land, but may also be responsible for some of the raiding taking place.

Therefore, in the next section in which the behaviour of the baboons is examined in relation to the raiding of farmland, the behavioural changes associated with raiding and farmer retaliation are expected to be found to a large extent in occasional leaver troops and to a lesser extent in leaver troops.

4.2 Behaviour

4.2.1 Recap of aims and predictions

The primary aim of the behaviour section of this study was to examine the behavioural responses of the troops in the reserve to raiding and farmer retaliation. It was predicted that

troops that raid farmland would display higher levels of aggression, self-grooming and mating and lower levels of foraging than troops that do not raid farmland. These changes were expected to be found to a large extent in occasional leaver troops, to a lesser extent in leaver troops, and not at all in non-leaver troops.

4.2.2 Aggression

There was no statistically significant difference in the levels of aggression displayed by the troops. However, leaver and occasional leaver troops consistently displayed around double the levels of aggression seen in non-leaver troops, with the exception of two of the occasional leaver troops (AS43 and AS55), both of which were observed for very low quantities of time. It seems likely that this lack of statistical significance is a factor of the small sample sizes involved. This, however, cannot be determined without further study. If present, an increase in aggression amongst leavers and occasional leavers could indicate an increase in social instability due to the killing of individuals by farmers and an increase in the immigration of new males (Pereira, 1983; Beehner et al., 2005; Bergman et al., 2005).

4.2.3 Self-grooming

Self-grooming was most common in leaver troops and least common in occasional leaver troops. While the high levels of self-grooming in leaver troops was predicted, and may indicate increased stress in these troops (Maestripieri et al., 1992), the very low levels of self-grooming in occasional leavers and the high levels of self-grooming in non-leavers were contrary to expectations. It may be that the use of the reserve as a refuge allows occasional leavers to avoid farmer retaliation to a large extent, allowing them to gain the benefits of raiding without the disadvantages. Another option, however, is that self-grooming is not an accurate indicator of the sorts of stress being experienced. The sources of stress expected to be experienced by raiding baboons (increased immigration of new males, loss of troop members and increased social instability) have been related to increases in glucocorticoid levels (Beehner et al., 2005; Bergman et al., 2005 & Engh et al. 2006) but not to increased levels of self-grooming, which is merely considered to be a general indicator of stress in primates (Maestripieri et al., 1992) and an indicator of relationship uncertainty in baboons (Castles et al., 1999). Self-grooming may also be being affected by some other factor such as parasite load, which also stimulates self grooming in primates (Zamma, 2002).

4.2.4 Mating

There were no statistically significant differences in the levels of mating displayed by the troops. However, mating was consistently more common in occasional leavers than in leavers and non-leavers, with the exception of occasional leaver troop AS55, which was only observed on 1 occasion. The lack of significance may be due the low sample sizes involved, or there may simply be no relationship between mating and raiding behaviour. If present, an increase in mating among occasional leavers would most likely indicate an increase in growth and reproduction due to increased foraging efficiency and food quality (Strum, 1994) or an increase in female reproductive cycling due to harassment induced miscarriage and infanticide by immigrant males (Pereira, 1983; Beehner et al., 2005).

4.2.5 Foraging

Foraging was most common in non-leaving troops and least common in leaving troops, with occasional leavers occurring between them. The results therefore confirm the prediction that raiding troops would spend less time foraging inside the reserve than non-raiding troops due to an increase in raiding outside the reserve. Occasional leavers foraged less than leavers. However, the leaver troops spent around half their time outside the reserve, giving them plenty of time to make up their remaining food requirements foraging on both fallow land and cultivated land. The occasional leavers, on the other hand, spent <5 % of their time outside the reserve, yet still foraged less than non-leavers, suggesting that they were foraging primarily on cultivated land when outside the reserve in order to make up their remaining food requirements in a mere 2 - 5 % of their time. The behaviour of the occasional leavers is similar to that observed by Cowlishaw (1997a & b) who found that troops would forage intensively in resource rich, high risk area, while spending most of their time in low risk areas.

4.2.6 Other behaviours

Although there were no significant differences in the levels of vigilance between leaving categories, levels of vigilance observed for non-leavers were lower than those observed for the leaver and occasional leaver troops, with the exception, once again, of the two occasional leaver troops AS43 and AS55, both of which were observed for very short times. If present, an increase in vigilance among leaver and occasional leaver troops could indicate that a general fear of humans continued to affect them even inside the reserve, as

most vigilance observed was directed at hikers (pers. obs.). Observed levels of socio-positive behaviour and motor play were roughly equal across the three leaving categories.

4.2.7 Conclusions

The behavioural data show that those troops (leaver and occasional leaver) indicated to be raiding farmland by the space use data, are indeed foraging less than non-leavers within the reserve, reinforcing the conclusion that these troops are potentially obtaining food elsewhere. The evidence for behavioural changes related to farmer retaliation, however, is not strong. While raiding and farmer retaliation may be resulting in increased aggression, mating and even vigilance, none of these behaviours were significantly different among the troops. More data would be needed in order resolve this matter. The data for self-grooming are more obscure, with the occasional leavers (thought to be the group most responsible for raiding farmland) displaying significantly less self-grooming than leavers and non leavers. This lack of clear patterns suggests that levels of farmer retaliation and resulting social instability may be fairly low.

4.3 Questionnaire survey

4.3.1 Recap of aims and predictions

The primary aim of this section of the study was to investigate raiding patterns of baboons as experienced by farmers and to assess levels of farmer retaliation. It was expected that maize would be especially targeted and that raiding would be most common in the early and late dry season, due to the availability of maize and natural food shortages.

4.3.2 Patterns of raiding

Most farmers around Suikerbosrand Nature reserve did experience some level of raiding. Only maize and bean farmers reported significant losses and these items tended to be raided more frequently than other items as well as being raided throughout the year. Other items such as garden fruit and vegetables, garbage, eggs and animal fodder were raided less often, and mainly during the winter. Though most of the data could not be statistically analysed, the general pattern that emerges is one of baboons raiding favoured crops (maize and beans) whenever possible, with natural food shortages in the winter increasing the frequency of raiding and the range of items raided.; and increased raiding of other items during periods of natural scarcity and were capable of feeding on a wide range of anthropomorphic food. This matches the findings of Naughton-Treves et al. (1998) who found

that baboons prioritised maize over natural forage, increased raiding of other items during periods of natural scarcity and were capable of feeding on a wide range of anthropomorphic food. Naughton-Treves et al. (1998) also found that baboons fed on maize throughout its life cycle, eating seedlings, inflorescence, pith and fruit. This may explain why farmers reported year-round losses of maize and beans. Also, Segal (2008) found kernels of maize in the faecal matter of the troops throughout the year, indicating that farmers do not securely store their grain after the harvest, making it available long after the early dry season. The information from the farmers also supports the findings of Segal (2008) that the Suikerbosrand baboons respond to the scarcity of food in the dry season by widening their diet.

It appears that the baboons were not acting in ways threatening to people, with the only two claims of baboons behaving threateningly being indicative of a perceived, rather than actual threat. This matches previous findings of baboons being seen in a somewhat unrealistically negative light, such as being described as crafty, malicious and a menace to women and children (Naughton-Treves, 1997). The baboons do, however, appear to pose a very real threat to dogs, with many reports of pet dogs being killed volunteered by farmers in their questionnaires.

4.3.3 Patterns of retaliation

Most farmers in the area claimed not to shoot baboons. While some farmers may be reluctant to report the killing of baboons, a low level of farmer retaliation would help to explain the weak evidence for behavioural changes predicted to result from it. On the other hand, no farmers reported using traps or snares, despite the presence in the reserve of several baboons with missing hands or feet (pers. obs.), suggesting an under-reporting of retaliation. Though not statistically tested, the perception of baboons as dangerous, the suffering of large financial losses and the loss of dogs all appear to increase the likelihood of farmers resorting to lethal retaliation. This supports the findings of Holmern et al. (2007) that greater losses to raiding animals leads to an increase in the approval of lethal retaliation. There also appeared to be some tendency towards the targeting of large males, which would increase the social disruption associated with the loss of troop members. In addition to shooting baboons, many farmers reported a range of other techniques to prevent raiding, such as electric fencing, dogs and scaring the baboons away with loud noises and bright lights. Although there was often a wide range in the reported effectiveness of the same techniques being used by different farmers, no techniques (including shooting) appear to be very effective. No farmers seem to have found a reliable method of preventing raiding. This matches the experiences of farmers

elsewhere, such as around Kibale National Park in Uganda, where most farmers must guard their crops constantly to prevent raiding by olive baboons and other large mammals (Naughton-Treves, 1997).

4.4 Overall conclusions

My study suggests that the troops primarily responsible for raiding farmland around the Suikerbosrand Nature reserve are the occasional leaver troops. These troops appear to be using the reserve as a refuge, making short forays out of the reserve during which they forage intensively on cultivated land. This is indicated by the small amount of time spent outside the reserve by these troops, their low levels of foraging within the reserve and their high space use overlaps with other troops. The leaver troops appear to be shifting their home ranges out of the reserve to forage on fallow land, though they are also likely to be raiding farmland to some extent. This is indicated by the large amount of time spent outside the reserve by these troops, their low levels of foraging within the reserve, and their low space use overlaps with other troops. Raiding behaviour is therefore present in most of the reserve's troops, as only two of the troops studied did not seem to be responsible for any raiding at all.

The raiding behaviour appears to be driven by both the limited food supply within the reserve and the preference of the baboons for certain crops (maize and beans) over naturally available forage. This is indicated by the reports from farmers of the raiding of maize and beans whenever they are available and the increased amounts and varieties of items reported to be targeted by baboons in the dry season. The need for leaver troops to forage on non-cultivated land outside the reserve despite the added risks involved also indicates that the limited food supply within the reserve is affecting the troops.

Levels of lethal retaliation as reported by farmers are low, but nonetheless present. Farmers also reported a tendency towards the targeting of large males.

The presence of behavioural changes in raiding troops related to farmer retaliation is not clear. However, it is the author’s opinion, based on the data available, that there is some degree of social disruption in raiding troops resulting from the loss of troop members. Further study would be necessary in order to clarify the matter.

4.5 Recommendations

Control techniques often work through increasing the costs and/or decreasing the benefits of foraging in areas of human activity, so as to make foraging on natural land the more appealing option (Strum, 1994). Such methods include shifting cultivars to something

less appealing to baboons (Naughton-Treves et al., 1998; Strum, 1994) and guarding crops using lethal or non-lethal means to increase the risk of raiding and/or to reduce foraging success on farmland (Falls, 1993; Naughton-Treves, 1997).

In areas where high populations of leaving animals are thought to be compounding the problem, culling is often considered (Falls, 1993). Alternatives to large scale culling include the selective killing of problem animals and the translocation of problem troops to areas far from farmland (Falls, 1993); translocation has been successfully conducted with two wild olive baboons troops (Strum, 2005). My study suggests that any such efforts should focus on the occasional leaver troops, as these are likely to be responsible for the majority of raiding behaviour. In the future, this 'occasional leaving' behaviour, as well as low levels of foraging within the reserve could indicate raiding behaviour. Radio telemetry and behavioural observations could therefore be used as a way to identify problem troops.

The responses from farmers in this study indicate that some troops may be preferentially raiding maize, regardless of the availability of non-anthropogenic food. Reducing the baboon population is therefore unlikely to be a cure-all solution. Other solutions that could be worth investigating include learned food aversion (Gill et al., 2000; Baker et al., 2005; Baker et al., 2007; Cox et al., 2004; Nicolaus & Nellis, 1987; Zahorik et al., 1990) and the switching of crop species grown (Parker & Osborn, 2006) or the guarding of crops (Naughton-Treves, 1997) by farmers.

4.6 Future studies

In this study, the troops were grouped together into 3 categories (leavers, non-leavers and occasional leavers) in order to examine trends relating to raiding behaviour. Future studies could examine troops on an individual basis to provide a finer resolution of the response of different troops to the opportunity to raid farmland around the Suikerbosrand. For example, occasional leaver troop AS42 was found by Segal (2008) to have far higher quantities of maize in its faeces than any other troop, and may be a prime candidate for translocation.

If the reserve management requires troop specific data on troop raiding behaviour, it would also be useful to question farmers about raiding by baboons and shooting of baboons without the drawback of anonymity. In this study, anonymous questionnaires were sent to farmers so that they would not be hesitant to admit to the shooting of baboons. This, however, made it impossible to match up reports of raiding and farmer retaliation to specific farms, and thereby to specific troops. If farmers were willing to provide such information without

anonymity, it would be possible to determine exactly which troops are responsible for the varying amounts of raiding reported, and which troops are losing members to lethal retaliation from farmers.

More extensive behavioural sampling would help to resolve the question of whether the social order of troops is being disrupted due to farmer retaliation, as the data on aggression, mating and vigilance remain inconclusive in this study due to the low sample sizes involved. More accurate census data would also be useful in assessing the impacts of farmer retaliation as the lack of reliable data on age and sex ratios in the last census made it impossible to determine if these demographic parameters were being affected.

A longer term study would allow for a more detailed analysis of seasonal patterns in raiding behaviour and of the environmental conditions (e.g. wet or dry years) that promote raiding behaviour. It may also provide information on how baboon troops develop raiding behaviour - Does raiding behaviour develop quickly or over many years? Does it spread between neighbouring troops or does it arise spontaneously when the opportunity presents itself?

Future studies could also focus on predation experienced by baboons, for example by brown hyena and black eagles.

Finally, future studies could investigate alternatives to culling and relocation. Learned food aversion trials could be carried out to test its effectiveness on baboons, and cost benefit analyses could be used to examine the financial and practical feasibility of farmers switching crop species or employing people to guard their crops.

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Appendix 1

Adjusted residuals of matrices of inter-monthly, intra-troop space use overlap

Adjusted Residual of Matrix for non-leaver troop AS33

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**2.11**	**2.15**	1.28	1.95	0.40	0.17	-0.06	0.87	-0.10	0.39	0.56	0.40
April	**2.13**	*	1.50	1.35	1.23	0.25	0.00	0.69	0.36	0.49	1.05	0.90	0.56
May	**2.13**	1.46	*	1.10	**2.83**	0.17	0.34	-0.40	1.63	-0.62	-0.06	0.16	0.20
June	1.28	1.32	1.09	*	1.94	0.55	0.29	0.33	0.47	0.38	1.02	0.95	0.07
July	1.92	1.17	**2.84**	1.84	*	0.38	-0.18	-0.64	1.54	-0.58	-0.11	0.01	-0.09
Aug	0.37	0.14	0.08	0.63	0.38	*	**2.08**	1.75	1.05	1.40	0.45	1.07	0.06
Sept	-0.02	-0.30	0.19	0.25	-0.44	**2.15**	*	1.41	1.16	**2.19**	1.31	1.12	-0.28
Oct	0.05	0.81	-0.37	0.56	-0.57	1.79	1.47	*	0.84	**2.05**	1.28	1.61	0.44
Nov	0.77	0.06	1.78	0.34	1.67	0.91	1.05	0.56	*	0.01	-0.11	0.32	-0.94
Dec	-0.16	0.48	-0.82	0.51	-0.71	1.46	**2.18**	**2.10**	0.26	*	**2.42**	1.52	0.05
Jan	0.31	1.06	-0.26	1.09	-0.27	0.40	1.29	1.17	0.06	**2.36**	*	1.69	-0.27
Feb	0.51	0.87	0.00	1.01	-0.13	1.03	1.10	1.52	0.45	1.43	1.68	*	-0.09
Total	-0.02	-0.22	-0.39	0.41	-0.40	0.14	0.48	-0.65	0.41	-0.18	0.14	0.38	0.12

Adjusted Residuals of Matrix for leaver troop AS35

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**3.52**	1.68	0.28	1.37	1.23	-0.76	-3.04	-3.68	-1.32	**2.59**	**4.75**	0.32
April	**3.72**	*	1.76	0.77	1.00	1.24	-0.56	-1.73	-1.51	-0.28	1.54	**3.19**	0.26
May	1.52	1.81	*	1.74	**2.04**	1.06	0.83	-0.42	-0.28	-0.79	-0.34	1.37	-0.49
June	-0.46	0.60	1.55	*	0.37	0.78	1.68	1.36	0.86	0.62	1.11	0.72	-0.24
July	1.03	0.88	1.96	0.35	*	1.68	1.78	1.04	1.00	0.11	-1.41	-0.64	-0.68
Aug	0.79	1.16	1.07	0.90	1.61	*	1.36	0.22	1.20	0.88	0.32	0.34	0.34
Sept	-1.53	-0.59	0.79	1.62	1.56	1.24	*	**2.79**	**2.45**	1.64	0.05	-0.98	-0.13
Oct	-3.12	-1.21	-0.04	1.14	0.85	0.21	**2.29**	*	**5.11**	**3.11**	-0.18	-1.55	-0.65
Nov	-3.28	-0.81	0.21	0.90	0.92	1.06	**2.05**	**4.92**	*	**3.36**	-0.37	-1.42	0.06
Dec	-1.65	-0.16	-0.23	0.64	0.28	0.73	1.42	**3.15**	**3.46**	*	1.47	-0.23	0.24
Jan	**2.02**	1.33	0.16	1.16	-0.59	0.46	0.31	-0.02	-0.45	1.67	*	**2.89**	0.60
Feb	**4.66**	**2.92**	1.36	0.94	-0.16	0.49	-0.69	-1.76	-1.96	-0.16	**3.34**	*	0.57
Total	-2.61	0.58	1.26	1.00	0.79	0.67	0.56	-0.77	-1.28	0.21	-0.22	0.02	0.20

Adjusted Residuals of Matrix for leaver troop AS36

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**2.64**	1.45	0.63	-2.29	0.20	-0.84	0.91	0.95	**2.43**	**2.15**	1.09	-0.02
April	**2.64**	*	**2.36**	0.48	-2.05	0.06	-1.18	0.76	0.83	**2.76**	1.74	0.43	-0.30
May	**2.02**	**2.86**	*	**5.98**	-7.08	**3.07**	-5.66	0.31	1.44	**3.52**	0.42	-1.16	-0.96
June	0.70	0.62	**5.84**	*	-3.44	**3.10**	-3.05	0.30	1.48	1.51	0.15	-0.46	-0.76
July	-1.32	-1.13	-4.30	-1.92	*	-0.68	**11.83**	1.77	0.82	-2.10	0.11	**2.52**	1.04
Aug	0.35	0.30	**2.33**	**2.71**	-0.67	*	-1.10	1.45	1.71	0.71	0.25	0.38	0.40
Sept	-1.28	-1.41	-4.91	-2.64	**14.49**	-1.70	*	1.76	-0.28	-2.64	-0.44	**3.25**	-0.70
Oct	0.31	0.23	-0.92	-0.32	**3.29**	0.89	**3.40**	*	0.76	-0.03	0.60	**2.05**	0.43
Nov	0.54	0.48	0.47	1.05	1.61	1.42	0.34	0.95	*	0.94	1.02	0.83	-0.01
Dec	**2.58**	**2.89**	**3.14**	1.59	-3.44	0.85	-2.63	0.81	1.53	*	1.70	0.15	0.10
Jan	1.94	1.59	-0.29	0.04	0.51	0.04	0.44	1.09	1.28	1.34	*	1.85	0.48
Feb	0.41	-0.13	-2.40	-1.07	**4.49**	-0.41	**5.40**	1.89	0.56	-0.72	1.32	*	0.34
Total	-0.44	-0.19	-3.93	-0.95	0.86	-1.18	2.05	2.16	1.41	-1.34	-0.31	1.92	0.05

Adjusted Residuals of Matrix for non-leaver troop AS39

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**3.29**	1.53	-0.09	0.69	-0.48	0.83	0.94	1.18	-0.28	0.50	-0.02	-0.61
April	**3.27**	*	1.65	-0.36	0.45	0.03	0.77	0.73	1.31	-0.01	0.54	0.34	-0.36
May	1.62	1.74	*	0.66	0.76	0.59	0.29	0.25	0.84	0.67	1.34	1.15	0.22
June	0.08	-0.22	0.74	*	1.89	**2.68**	-0.83	-1.07	-0.32	1.67	1.69	1.48	-0.33
July	0.78	0.54	0.74	1.70	*	1.86	0.28	0.29	0.74	0.84	0.46	1.35	0.16
Aug	-0.01	0.38	0.77	**2.33**	1.87	*	0.44	0.08	0.84	0.97	0.58	1.50	0.77
Sept	0.80	0.75	0.35	-0.47	0.34	0.27	*	**4.03**	**2.20**	0.05	-0.15	0.44	0.26
Oct	0.88	0.74	0.35	-0.58	0.37	0.00	**4.00**	*	**2.20**	0.11	-0.07	0.49	0.29
Nov	1.08	1.19	0.72	-0.27	0.66	0.57	**2.45**	**2.46**	*	0.28	-0.01	0.64	0.26
Dec	-0.25	0.02	0.67	1.66	0.89	0.90	-0.21	-0.17	0.26	*	**3.03**	1.50	-0.37
Jan	0.57	0.60	1.45	1.76	0.41	0.33	-0.65	-0.57	-0.22	**3.19**	*	1.29	-0.48
Feb	0.15	0.46	1.15	1.35	1.38	1.46	0.45	0.48	0.76	1.40	1.19	*	0.41
Total	0.27	0.39	0.44	-0.44	0.28	-0.76	-0.54	-0.74	0.29	0.21	0.44	0.37	0.21

Adjusted Residuals of Matrix for leaver troop AS41

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**2.25**	1.40	0.81	1.13	-0.47	-0.10	1.24	0.09	0.14	-0.48	0.66	-0.59
April	**2.06**	*	**2.37**	0.84	1.74	1.34	0.21	0.01	-0.05	0.23	-0.14	0.62	0.08
May	1.37	**2.59**	*	1.17	0.89	0.57	0.71	0.40	0.34	0.63	0.30	0.70	0.23
June	0.91	1.12	1.36	*	-0.39	-0.49	1.40	1.20	1.51	1.40	1.27	0.60	0.15
July	0.55	1.06	0.40	-0.36	*	**7.14**	-0.14	-0.61	-0.50	-0.16	-0.22	0.13	-0.10
Aug	-0.23	0.82	0.34	-0.17	**5.94**	*	0.01	-0.28	-0.28	0.01	-0.05	-0.40	-0.08
Sept	-0.16	0.36	0.84	1.41	0.04	-0.05	*	1.62	1.58	1.48	1.66	0.69	0.00
Oct	1.48	0.07	0.47	1.25	-0.93	-0.81	1.70	*	1.88	1.17	1.80	1.35	-0.03
Nov	0.08	0.05	0.44	1.61	-0.66	-0.75	1.68	1.90	*	1.80	**2.12**	1.36	0.03
Dec	0.08	0.34	0.71	1.39	-0.06	-0.12	1.47	1.11	1.69	*	1.45	1.02	-0.20
Jan	-0.56	-0.02	0.42	1.32	-0.06	-0.15	1.70	1.76	**2.04**	1.51	*	1.80	0.13
Feb	0.78	0.93	0.89	0.69	0.64	-0.77	0.76	1.31	1.29	1.08	1.73	*	0.25
Total	-0.90	0.42	0.20	0.21	0.91	-0.35	-0.09	0.20	0.00	0.00	-0.17	-0.57	-0.13

Adjusted Residuals of Matrix for occasional leaver troop AS42

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**4.14**	**8.62**	**6.57**	**3.38**	-2.16	-3.43	-2.27	-3.76	-2.91	-2.99	-0.42	-0.76
April	**3.71**	*	**6.78**	**3.09**	**4.88**	-3.63	-1.48	-1.58	-1.03	-0.75	-3.28	0.75	1.12
May	**7.12**	**6.83**	*	**7.33**	**4.83**	-3.56	-4.18	-2.74	-4.10	-3.17	-3.27	0.72	0.44
June	**5.30**	**2.86**	**6.97**	*	**3.82**	0.34	-3.04	-1.42	-3.50	-2.53	-1.28	0.58	1.43
July	**3.10**	**4.82**	**4.88**	**3.97**	*	0.79	-2.14	-1.05	-2.12	-1.55	-2.21	0.82	1.12
Aug	-0.24	-2.08	-1.72	0.96	1.41	*	1.28	1.87	0.76	0.81	**2.41**	1.09	0.83
Sept	-2.16	-1.48	-4.27	-3.26	-1.69	1.70	*	**3.76**	**5.28**	**4.48**	**3.78**	1.52	-0.18
Oct	-1.41	-2.06	-3.02	-1.64	-0.82	**2.46**	**3.59**	*	**3.84**	**3.00**	**2.75**	1.85	-0.21
Nov	-2.72	-1.04	-4.52	-4.18	-1.86	0.82	**5.55**	**4.17**	*	**5.49**	**4.01**	1.27	-0.63
Dec	-2.02	-0.85	-3.54	-3.08	-1.34	0.72	**4.62**	**3.22**	**5.43**	*	**3.55**	1.34	-0.24
Jan	-2.75	-5.10	-4.46	-1.88	-2.87	**4.02**	**4.09**	**3.02**	**4.16**	**3.70**	*	1.93	-2.50
Feb	0.13	0.67	1.05	0.70	1.16	0.61	0.89	1.55	0.62	0.83	1.59	*	0.31
Total	2.54	0.40	1.41	1.92	2.70	-3.61	-2.09	-0.24	-2.06	-0.89	-1.31	1.96	0.73

Adjusted Residuals of Matrix for occasional leaver troop AS43

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**2.37**	1.32	0.21	0.82	0.23	0.62	0.90	0.35	1.54	0.40	0.48	0.17
April	**2.45**	*	1.26	0.51	0.61	0.17	0.93	1.33	0.21	0.42	0.42	0.41	-0.33
May	1.36	1.33	*	1.77	1.14	1.07	0.94	1.09	0.42	0.04	0.38	0.10	0.33
June	0.20	0.60	1.71	*	1.25	1.21	0.59	0.40	1.02	0.22	1.24	1.14	0.25
July	0.70	0.57	1.03	1.22	*	1.84	1.01	0.91	0.84	0.24	0.13	0.53	-0.43
Aug	0.11	0.20	0.98	1.19	1.81	*	1.02	0.79	0.97	0.82	0.89	0.79	-0.04
Sept	0.49	0.94	0.83	0.47	1.05	1.02	*	**2.16**	1.46	0.26	0.14	0.43	-0.30
Oct	0.85	1.38	1.02	0.25	0.95	0.78	**2.16**	*	1.36	0.54	-0.05	-0.08	-0.30
Nov	0.20	0.19	0.23	0.96	0.86	0.94	1.41	1.31	*	1.05	0.84	1.30	-0.24
Dec	1.48	0.55	0.06	0.26	0.45	0.88	0.45	0.65	1.09	*	1.96	1.61	0.36
Jan	0.45	0.58	0.40	1.21	0.40	0.95	0.39	0.24	0.92	1.92	*	**2.03**	0.49
Feb	0.47	0.51	0.08	1.10	0.66	0.83	0.56	0.14	1.28	1.60	**2.07**	*	0.22
Total	-0.29	0.17	-0.35	-0.20	0.55	0.30	0.53	0.46	0.41	-0.44	-0.60	-0.35	0.19

Adjusted Residuals of Matrix for occasional leaver troop AS44

	Sept	Oct	Nov	Dec	Jan	Feb	Total
Sept	*	**5.52**	**6.59**	-0.80	-1.61	-3.14	-0.83
Oct	**5.92**	*	**6.01**	0.18	-0.92	-2.24	-0.10
Nov	**6.73**	**5.75**	*	0.00	-1.35	-3.15	-0.22
Dec	-0.82	0.61	0.14	*	**5.00**	**5.13**	0.50
Jan	-1.88	-0.70	-1.64	**5.30**	*	**7.93**	0.35
Feb	-2.90	-1.36	-2.99	**5.86**	**8.13**	*	0.16
Total	-0.34	0.77	-0.09	0.98	0.59	-2.05	-0.14

Adjusted Residuals of Matrix for occasional leaver troop AS45

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	1.78	1.14	1.45	0.56	-0.46	-1.06	-0.06	0.64	1.88	**2.52**	1.42	0.01
April	1.80	*	**2.63**	1.63	0.40	-1.24	-1.63	-0.24	0.67	**2.12**	1.96	1.15	-0.07
May	1.30	**2.60**	*	1.57	0.12	-1.86	-0.12	**2.04**	1.44	1.55	-1.21	0.45	-0.10
June	1.46	1.61	1.48	*	0.77	-0.54	-0.18	0.39	0.50	0.95	1.27	1.25	-0.25
July	0.60	0.33	-0.22	0.81	*	**2.15**	1.53	0.59	1.33	0.53	1.09	1.28	0.49
Aug	-0.42	-1.39	-2.48	-0.50	**2.10**	*	**7.16**	1.66	1.14	-0.67	-0.23	0.45	-0.10
Sept	-0.60	-1.28	-0.12	0.15	1.60	**6.54**	*	**5.16**	1.49	-1.12	-3.86	-1.23	0.32
Oct	0.28	0.00	**2.09**	0.66	0.80	1.73	**5.17**	*	**2.62**	0.29	-4.57	-1.09	0.41
Nov	0.64	0.57	1.32	0.49	1.29	1.14	1.38	**2.68**	*	0.85	-0.62	0.00	0.19
Dec	1.89	**2.13**	1.45	0.96	0.50	-0.68	-1.63	-0.03	0.86	*	**2.45**	1.62	-0.11
Jan	**2.43**	**2.02**	-0.79	1.48	1.34	0.29	-3.07	-3.63	0.12	**2.38**	*	**3.68**	-0.18
Feb	1.41	1.09	0.14	1.23	1.24	0.42	-1.80	-1.65	-0.01	1.61	**4.28**	*	-0.58
Total	0.99	0.17	-1.34	0.72	1.19	0.57	-0.67	-0.66	1.24	0.75	-3.37	0.44	0.03

Adjusted Residuals of Matrix for occasional leaver troop AS55

	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
March	*	**2.27**	0.82	-0.45	-0.17	-0.56	0.14	0.72	1.27	1.68	0.81	1.07	-0.83
April	**2.32**	*	1.25	0.09	0.22	0.04	0.51	0.89	1.20	1.36	0.49	1.26	0.21
May	1.00	1.37	*	**2.58**	1.82	1.78	0.23	0.04	-0.10	-0.22	-0.13	0.56	-0.23
June	-0.16	0.23	**2.57**	*	**2.34**	**2.67**	0.70	-0.07	0.11	-0.91	1.41	0.09	0.20
July	-0.15	0.11	1.84	**2.37**	*	**2.48**	0.86	0.23	0.13	-0.47	0.57	0.28	-0.53
Aug	-0.44	0.03	1.81	**2.70**	**2.46**	*	1.22	0.60	0.13	-0.70	0.69	0.34	-0.12
Sept	0.31	0.51	0.30	0.53	0.85	1.11	*	**2.35**	0.75	0.06	1.08	1.72	0.05
Oct	0.83	0.85	0.10	-0.24	0.27	0.50	**2.25**	*	1.35	0.86	0.66	1.88	-0.09
Nov	1.32	1.14	0.09	0.03	0.27	0.17	0.72	1.31	*	**2.27**	1.45	1.16	0.45
Dec	1.53	1.27	0.22	-0.42	0.08	-0.15	0.35	0.93	**2.04**	*	0.91	0.95	0.38
Jan	1.02	0.62	0.18	1.21	0.69	0.71	1.11	0.81	1.57	0.96	*	0.97	0.65
Feb	1.17	1.24	0.53	-0.11	0.30	0.25	1.64	1.89	1.18	0.88	0.83	*	0.06
Total	0.29	0.22	0.53	-0.48	0.36	0.05	0.23	0.29	0.15	-1.55	-0.43	0.53	0.20