Foraging behaviour and diet in chacma baboons in Suikerbosrand Nature Reserve

Candice Segal

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Declaration

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

Candice Segal

Abstract

Foraging behaviour describes the mechanisms and decisions animals use to maximise energy gain. Baboons are a successful and widespread primate species in Africa, largely because of their ability to modify their broad omnivorous diet and foraging behaviour under changing environmental and climatic conditions. The population size of baboons found in the Suikerbosrand Nature Reserve, South Africa, has risen at a constant rate over the past few years, resulting in growing concerns of insufficient resources in the reserve to sustain the population. The aim of my study was to investigate foraging behaviour and diet in relation to the spatio-temporal fluctuations of resources in this isolated population of baboons. For my study, one individual in each of 10 different troops was fitted with a cell phone collar so that troops could be located daily using GPS data.

Diet, which was assessed by faecal analysis, showed a wide variety of components in the dry season (e.g. fruit and seed 48%, plant matter 29%, invertebrates 5%, maize 8%). In contrast, diet in early and late rain seasons was restricted to fewer components: plant matter (61%) in early rain and fruit and seeds (55%) in late rain season.

Contrary to my predictions, foraging behaviour, assessed through direct observation indicated that baboons foraged conservatively in the dry season when food resources are lower, spending more effort manipulating food and consuming comparatively less food. In the early and late rain seasons when food resources were greater, baboons spent more effort actively searching, manipulating and consuming food.

Similarly, GPS data revealed that baboons travelled further in the early and late rain seasons than in the dry season. Baboons in the Suikerbosrand Nature Reserve appear to increase foraging effort by travelling more and selecting habitats where food resources are both abundant and energy rich. When resource availability was low, baboons tended to reduce energy expenditure by travelling less, selecting habitats with more reliable resource availability and consuming whatever foods were available.

Home range size remained constant, showing no seasonal or spatial pattern but seasonal habitat use in troops varied, depending on habitat type. For example, in the dry season, troops preferred woodland and shrubland habitat over grassland but in the early rain season, habitat use in grasslands increased. This is most likely due to the increase in plant growth in grasslands.

In conclusion, my study set out to investigate various aspects of foraging behaviour in a widespread and well researched primate species. My findings not only confirm our knowledge of the adaptability of baboon foraging behaviour and diet but provide new insight into foraging strategies in a seasonal environment as well as the underlying mechanisms influencing behavioural responses in baboons. The influence of changing spatial factors (e.g. habitat availability and resource quality) is less clear at a population scale and further studies are needed to better understanding of the influence of spatial changes in resources on foraging behaviour and troop dynamics. From my findings, I provide management advice, which can be used as an aid to manage the baboon population.

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Chapter 1: Introduction

1.1 Rationale for the study

Chacma baboons (*Papio hamadryas ursinus*) are a widespread and successful primate species in southern Africa (Estes 1992, Rowe 1996). The ability to live in many habitats, under challenging environmental conditions, is a major reason for their success (Altmann 1998). In South Africa, the rapid increase of urbanization and decreasing number of unprotected natural areas has caused many species, including baboons, to become scattered and isolated. This is the situation facing a population of chacma baboons in the Suikerbosrand Nature Reserve, a small mountainous grassland reserve situated in Gauteng Province.

Suikerbosrand Nature Reserve comprises ideal habitat for baboons with a range of different habitats such as open grassland, *Acacia* savannah, mixed shrub land and denser wooded areas. Challenges facing baboons include seasonal fluctuations and spatial changes in food availability with regard to habitat availability. Problems arise when a population grows too large for small areas of protected natural habitats. When the foraging needs imposed by baboons on natural resources are not sustainable, it is likely that baboons will look to adjacent human resources, such as farming or urban environments, to meet energy demands.

The opportunity arose to study this population because radio collars (which use cell-phone telemetry to receive information) were fitted onto several individual baboons by staff from the Gauteng Department of Agriculture, Conservation and Environment (hereafter referred to as GDACE). My project investigates the diet, foraging behaviour and movement patterns in the baboon population at Suikerbosrand Nature Reserve. The combined knowledge from different aspects of foraging will give an indication of foraging effort within the population with regards to seasonal and environmental changes in food resources. Using the results from this study, it is my aim to generate foraging models in relation to the foraging and activity pattern of baboons in Suikerbosrand Nature Reserve, which can be used as an aid to manage the baboon population there.

1.2 Diet

What an animal eats is directly tied to the environment which it inhabits and the type of food resources it can use (Robinson and Holmes 1982). Resources are not constant and fluctuate temporally (Hill and Dunbar 2002) and spatially (Klaassen *et al.* 2006). Baboons are described as generalist omnivores and their diet includes many types of plants, invertebrate and small vertebrate animals (Altmann and Altmann 1970). In omnivores, diet over a short period is rarely restricted to one type of food (Clark 1982).

Omnivores face multiple choices in food selection, where individuals may need to balance the ratio of food types in their diet in relation to overall energy needs and digestive ability (Buck *et al.* 2003, Clark 1982). For example, fruit is a high-energy food source and can be quickly utilized, but is seasonally abundant, distributed randomly in an area and habitat specific (DeVore and Hall 1965, Garber 1987). Therefore, the cost of energy and time expended in obtaining the fruit may outweigh its energy gain (Jolly 1985). Whereas plant material, such as leaves from grass species, is abundantly available and widespread but is low in nutrients and difficult to digest, containing high levels of secondary compounds (e.g. crude fibre and/or tannins; Chapman and Chapman 2002, Dunbar 1988, Wynne-Edwards 2001).

Baboons are able to select from not only the species or part of the plant to eat, but when to include certain food items in their diet (Hamilton *et al.* 1978). Seasonal trends in environmental variables influence plant and animal resource levels and availability within different habitat types, which will influence diet choice (Alberts *et al.* 2005). Rainfall is a major determinant of plant productivity, where seasonal patterns correspond with resource availability (Alberts *et al.* 2005). For example, in spring- new grass blades; in summer - seeds and rhizomes; in winter - roots, bulbs and tubers (Altmann and Altmann 1970, Post 1982).

1.3 Foraging behaviour

Foraging behaviour describes how an animal searches, locates, processes and consumes food resources from the environment (Cant and Temerin 1984, Mellgren and Brown 1987, Walker *et al.* 1999). This behaviour is an important part of an animal's daily activity budget, influencing its survival and reproductive success (Stephens and Krebs 1986). Animals are faced with many options when foraging, such as when or where to forage, what to forage on and for how long to forage (Kamil *et al.* 1987, Menzel and Wyers 1987). Therefore, foraging behaviour is associated with costs and benefits (Stephens and Krebs 1986). The obvious benefit is energy gain from food consumption. The cost, however, is energy expenditure from searching (locomotion, Rashotte *et al.* 1987), processing (chewing, digging, Altmann 1998) and consuming (digestion, Penry 1993).

Foraging behaviour is influenced by intrinsic and environmental factors, such as seasonal fluctuations in food availability (Bronikowski and Altmann 1996, Chouteau 2006), the effect of climatic changes on thermoregulatory needs (Iwamoto and Dunbar 1983, Schwaibold and Pillay 2006), inter- and intra-species competition (Barton *et al.* 1996, Shopland 1987), and predation pressure (Cowlishaw 1997, Lima 1987).

One of the most important foraging theories developed over the last century is Optimal Foraging Theory, which predicts that an animal forages in a manner that optimizes energy gain (Perry and Pianka 1997). Therefore, the study of foraging behaviour investigates the mechanisms and decisions used by animals to find enough food from the environment to meet energy requirements (Lewis *et al.* 2004, Owen-Smith 1994).

1.4 Foraging behaviour in baboons

Baboons are skilful and efficient foragers (Altmann 1998, Brownikowski and Altmann 1996, DeVore and Hall 1965). Altmann and Altmann (1970) stated that the success of baboons as generalist omnivores was most likely due to “their lack of highly specialized anatomical adaptations” (p.114). Nonetheless, they possess two important anatomical adaptations for feeding. Firstly, hand dexterity allows baboons to perform fine actions such as peeling, digging, plucking, picking and holding, allowing them to access many different food types (Altmann and Altmann 1970). Secondly, baboons use their cheek pouches for short-term food storage (Altmann 1998, Hayes *et al.* 1992). In habitats where food is clumped (e.g. fruit), cheek pouches enable a baboon to gather as much food as possible (Hayes *et al.* 1992). When resources are scattered (e.g. seeds), cheek pouches allow continued searching (Altmann 1998). Food stored in pouches is processed and consumed whilst the animal searches for the next item or during resting and social periods (Altmann 1998). The advantages of differential use of cheek pouches are decreased time for processing or consuming food and increased intake of food whilst foraging (Hayes *et al* 1992).

Baboons are active foragers and are comfortable in both terrestrial and arboreal habitats, travelling great distances over different types of terrain and inhabiting many different habitat types (Altmann and Altmann 1970, Rowe 1996).

In simple terms, baboons forage from ‘hand to mouth’ (Estes 1992). For example, when foraging on acacia seed pods, a baboon will first use its hands and/or mouth to tear pods from the tree, then the skin of the seeds is separated and pushed out by the tongue (Whiten *et al.* 1991). Baboons access a number of different food types by digging in different manners: to find tubers they dig deep holes; roots, rhizomes, insects and seeds need only shallow digging or scraping the surface (Estes 1992). Invertebrate species are located by turning over rocks and logs, tearing off bark or digging out holes (Estes 1992).

Baboons modify their foraging behaviour under different circumstances. Factors such as habitat type, resources availability, relative abundance of food and distribution of food, require different foraging strategies (Barton *et al.* 1992). Furthermore, foraging behaviour is influenced by seasonal variation in resource availability (Chouteau 2006). Environmental factors such as rainfall and temperature are known to influence food abundance (Bronikowski and Altmann 1996). Animals tend to spend more time foraging in seasons when food resources are limited compared to when food is abundant (Judas and Henry 1999, Owen-Smith 1994). Foraging and time spent travelling increases in times of lower rainfall and lower daily minimum temperatures, whereas with higher rainfall and higher daily temperatures, foraging and moving time decreases (Bronikowski and Altmann, 1996).

Baboons are social foragers, consequently foraging behaviour in an individual baboon is not only a response to its own needs but directly influenced by the needs of other troop members (Giraldeau and Caraco 2000). Individuals benefit from social foraging through increased vigilance against predators, improved food-finding and knowledge of habitat and resource availability (Altmann 1998, Galef and Giraldeau 2001, Sontag *et al.* 2006). A disadvantage of foraging in groups is increased competition for food (Shopland, 1987, Sontag *et al.* 2006). For example, as the number of troop members increases, the time needed for foraging by individuals also increases and consequently there is greater travelling behaviour to find sufficient food (Stacey 1986).

1.5 Distance travelled and foraging effort

Distance travelled gives an indication of energy expended through foraging (Moen *et al.* 1997). Seasonal availability of resources affects distance travelled (DeVore and Hall 1965), time spent foraging (Owen-Smith 1994) and consequently foraging effort (i.e. time and/or energy an animal allocates to foraging, required to meet energy needs under changing environmental costs, Abrams 1991). Byrne *et al.* (1993) found that mountain chacma baboons (*Papio hamadryas ursinus*) travelled further daily when food resource levels were at their lowest towards the end of winter, a pattern that occurs in many other mammals (Owen-Smith 1994). For example, foraging time and daily distance travelled for yellow baboons (*Papio hamadryas cynocephalus*) in Tanzania increased when rainfall and daily temperatures were low, whereas with higher rainfall and daily temperatures, foraging time and distance travelled decreased (Altmann and Altmann 1970, Bronikowski and Altmann 1996).

Distance travelled also gives an indication of foraging effort needed in different habitats. Habitat heterogeneity or uniformity within a troop's home range affects movement patterns: Henzi *et al.* (1992) found that, in habitats where resource dispersion is uniform that baboons spend less time travelling and more effort actively foraging. When resources are patchily distributed, foraging effort will reflect the distance needed to travel to reach food patches rather than time spent actively foraging (Noser and Byrne 2007). In addition, foraging effort and distance travelled may change depending on the size of the group, so that larger troops may need to forage for longer and travel further than smaller troops (Collins 1984, Fritz and Garine-Wichatitsky 1996).

1.6 Space Use

1.6.1. Movement patterns

Movement patterns describe how animals exploit spatially distributed resources (South 1999). At a small-scale, movement patterns describe an animal's foraging path within and between patches, whereas at a broad scale, movement patterns represent home range use and give an indication of resource patchiness or habitat heterogeneity (Nams 2005). Factors influencing space use may be environmental (habitat quality, distribution and abundance of resources, Shopland 1987), social or anthropogenic (urban encroachment, agriculture, Moyer *et al.* 2007).

In pioneering work on baboon behaviour and ecology, Altmann and Altmann (1970) noted that initially, movement patterns appeared random, since, over a short time span, baboons did not re-visit areas foraged. Over a longer time span, baboons foraged within a defined area (i.e. the home range; Altmann and Altmann 1970).

1.6.2. Home range

A home range is an area traversed by animals while foraging, mating and caring for young or an area used by an animal throughout its adult life (Jolly 1985, South 1999). Home range size is said to be influenced by habitat diversity, with animals in relatively homogeneous habitats having larger home ranges than those in areas with a greater diversity of habitats (Moyer *et al.* 2007). Seasonal changes in home range size are predicted to be inversely proportional to resource levels, so that larger home ranges are needed when food levels are low (Moyer *et al.* 2007, Phillips *et al.* 1998).

Baboons spend up to 70% of daily activity foraging and moving to different areas and/or foraging sites within their home ranges (Altmann and Altmann 1970, Post 1981). The size and shape are dependent on the following factors: size of troop, concentration of food and water, availability of shelter, proximity to other troops and other ecological factors (DeVore and Hall 1965, Stacey 1986).

Baboons do not appear to defend territories and it is common for home ranges of neighbouring troops to overlap significantly (approximately 63%, Stacey 1986, 52%, Anderson 1981). Yet, despite the high proportion of home range overlap, troops avoid contact with each other by using various strategies, such as using different core areas (DeVore and Hall 1965, Jolly 1985). If interactions occur, agonistic behaviour is rarely seen and troops will avoid aggressive encounters (DeVore and Hall 1965, Altmann and Altmann 1970).

1.6.3. Habitat use

Habitat use examines the behavioural responses of animals to changes in the environment at different spatial and temporal scales (Barton *et al.* 1992, Druce 2005). At a landscape level, animals must choose the type of habitat to utilise, which is influenced by food availability, abundance and quality (Druce 2005). Habitat selection over short time scales is likely to be influenced by seasonal availability and spatial dispersion food resources (Lucherini *et al.* 1995, Viera *et al.* 2005).

Different foraging models based on optimality theories are used to predict habitat selection and movement patterns to maximise energy gain relative to foraging cost (Barton *et al.* 1992, Stephens and Krebs 1986), for example patch use models (Charnov 1976).

Habitat use in omnivores such as baboons is influenced by factors such as energy needs (Mckenna 1982), distribution of food within a habitat (Barton *et al.* 1992), availability of cover from predators (Cowlishaw 1999), places to rest and access to water (Morris 1992). For example, Cowlishaw (1997) found that in chacma baboons (*Papio hamadryas ursinus*) in the Namib desert, high quality food resources were limited to habitat types in areas where predation risk was high, and in response, baboons selected habitats in areas where food quality was poorer and predation risk was lower. Habitat use, like foraging behaviour, is influenced by costs and benefits of changing environmental variables (Druce 2005).

1.7 Baboon-human interactions

1.7.1 Baboons and agriculture

Baboons are often pests of agriculture and are known to raid crops such as maize, harvested fruit, wheat, cassava and rice (Altmann and Altmann 1970, Hill 2000). Increasing occurrences of raiding occur when agricultural lands are found adjacent to conservation areas (Naughton-Treves *et al.* 1998). In addition, baboons are destructive feeders, consuming only parts of individual plants and, consequently causing high overall crop damage and financial losses to farmers (Naughton-Treves *et al.* 1998, Hill 2000).

Baboon raiding behaviour is reminiscent of their natural foraging behaviour, as it is opportunistic and selective (Naughton-Treves *et al.* 1998). Baboons were found to raid certain crops (maize) more frequently than others, while some farms were raided infrequently (Hill 2000). According to Anderson (1981), most troops in the Suikerbosrand Nature Reserve have been found to raid crops in the surrounding farmlands. In addition, raiding behaviour was highest during autumn and winter (Anderson 1981), coinciding with periods of low natural food availability.

1.7.2 Management and conservation principles

Management priorities have moved away from past conservation principles of preserving and managing species/populations (Southwick and Blood 1979) to preserving overall biodiversity (Garrott *et al.* 1993), emphasising ecosystem management (Simberloff 1999). Conflicting issues arise when previously conserved populations become overabundant and threaten current management aims of conserving overall ecosystem biodiversity (Garrott *et al.* 1993).

Management of overabundant populations is crucial, particularly when the success of a generalist or opportunistic species has become detrimental to other rarer species and to overall species diversity (Garrott *et al.* 1993). These rarer species are at a greater risk of increased inbreeding and decreased genetic diversity or extinction from random disease or drought events (Southwick and Blood 1979).

Active management of populations requires knowledge of species and habitat requirements (Druce 2005). However, management of populations is more difficult in areas where the requirements of human activities such as agriculture, logging, urban development and tourism, conflict with management techniques (Southwick and Blood 1979).

1.8 Aims

1. To assess the diet of troops in different areas of the reserve and over different seasons in Suikerbosrand Nature Reserve
2. To investigate the foraging behaviour of chacma baboons in Suikerbosrand Nature Reserve
3. To assess foraging effort in different areas of the reserve (spatial) and during different seasons (temporal) and the spatial and temporal interaction in foraging effort
4. To investigate temporal differences in troop foraging patterns in different areas of Suikerbosrand Nature Reserve.
5. To create a foraging model to assist management by providing:
    - understanding of influence of baboon foraging on biotic components within the Suikerbosrand Nature Reserve and raiding behaviour in the surroundings areas
    - recommendations to the Gauteng Department of Agriculture, Conservation and Environment with respect to baboon population density

1.9 Hypotheses and predictions

Hypothesis 1

An animal's diet choice should reflect the types of food, which are most accessible and give maximum energy return (Hughes 1993). Baboons are opportunist omnivores and their diet will reflect seasonal availability and preferences of food types (Barton and Whiten 1994). Diet will differ depending on the availability of food resources within their home range. Therefore, when food resources are abundant, the diet will contain fewer food types (i.e. a narrow diet); when food resources are limited, the diet will be broader.

Predictions

- Diet will be broader when resources are low in the dry season.
- Diet will be narrower in the early and late rain seasons when resources are abundant, and the diet will include food types that are abundantly available and most nutritious.

Hypothesis 2

In temperate grasslands, resource levels fluctuate over time (Alberts *et al.* 2005, *Cowling et al* 1997). Resource availability will be greater in the rainy season than in the dry season, resulting in baboons using different foraging strategies seasonally to meet energy requirements.

Prediction

- Foraging behaviours will differ seasonally. In the dry season, baboons will spend more time searching for and processing food resources that are more difficult to find and access. When food is abundant, following rain, baboons will consume more food, but search for and manipulate food less.

Hypothesis 3

Baboons are social foragers. The benefits of foraging in groups include increased vigilance against predators and location of food resources (Fritz and De Garine-Wichatitsky 1996). However, major predators (e.g. leopard) have been absent in Suikerbosrand Nature reserve for many years. Therefore, the costs of foraging in larger groups (Stacey 1986) may be greater than the benefits.

Prediction

- Foraging behaviour varies: individuals in larger troops will forage more than in smaller ones.

Hypothesis 4

Foraging effort will reflect the energy need imposed by external factors (Korstjens and Dunbar 2007). Distance travelled can be used as a surrogate measure of energy expended for foraging (Moen *et al.* 1997). Seasonal changes in climatic variables and resource availability will influence the energy demands on baboons and therefore their foraging effort.

Predictions

- Foraging effort will increase when energy needs are highest and decrease when energy needs are lower. Distance travelled will be greater in the dry season when food availability is low and when energy needs are highest. Distance travelled will decrease in the early rainy seasons when food is readily available,
- Foraging effort will differ among troops depending on troop size and/or habitat availability. Distance travelled will be greater in larger troops than smaller ones. Troops with access to high quality resources (e.g. food, water and shelter) will travel less than troops with access to poor quality resources.

Hypothesis 5

Suikerbosrand Nature Reserve contains a number of different habitat types, which contain different resource types used by baboons. Foraging behaviour will reflect the availability and distribution of resources (Morris 1992). Moreover, habitat use will reflect spatial and seasonal variability of resource availability within troop home ranges (Wong *et al.* 2004).

Predictions

- Home range size will expand and contract seasonally, reflecting seasonal variation in food availability. Therefore, home range size will be larger in the dry season when resources are scattered and smaller when resources are abundant.
- Troop home ranges will differ according to troop size and habitat availability.

- When resource distribution is clumped, home range use will be opportunistic and habitat specific. When resources are widespread or scattered, home range use will be varied and non-specific. Moreover, temporal changes in habitat use will reflect seasonal availability of specific resources. For example, when fruit is available, habitat use will be greater in areas when fruit is present.

Hypothesis 5

When resources are low, baboons will consume alternative sources of food (e.g. maize) from outside the reserve.

Prediction

- Crop raiding and inclusion of maize in the diet is likely to be variable, depending on the availability and/or when energy needs are greatest. Therefore, crop raiding will be opportunistic, especially in troops located near the edge of the reserve, close to neighbouring farms.

Chapter 2: Materials and Methods

2.1 General

2.1.1 Study Animal

The chacma baboon is the largest of the five subspecies of the genus *Papio* (Rowe 1996). It is distributed in many areas of southern Africa, inhabiting many different habitat types such as savannah, mountains, woodland, grassland, semi-desert and coastal areas (Roberts 1951, Rowe 1996).

The coat colouring ranges from yellowish-grey to dark brown (Rowe 1996). Male chacma baboons are larger than females, weighing 20 kg and 16 kg on average respectively and with a body length of between 765mm and 587 mm respectively (Rowe 1996).

Chacma baboons live in multi-male and multi-female troops (Dunbar and Barrett 2000). Dominance among males is usually decided by size and strength rather than by forming coalitions, so that the largest males have the greatest chance to mate (Dunbar and Barrett 2000). The hierarchy among females is decided by kinship bonds, where daughters inherit their mothers rank (Estes 1992).

Females and males reach sexual maturity at approximately 38 and 60 months respectively (Rowe 1996). Females have an oestrous cycle of approximately 35 days and develop prominent sexual swellings (Dunbar and Barrett 2000, Rowe 1996). Gestation lasts between 173-193 days (Rowe 1996). Chacma baboons do not have a specific breeding season and reproduce year round (Whiten *et al.* 1991). They have a lifespan of approximately 45 years (Rowe 1996).

2.1.2 Study site

The study was conducted in the Suikerbosrand Nature Reserve (E28.000dd, S26.000dd), situated approximately 40km south of Johannesburg near the farming town of Heidelberg. The reserve was originally approximately 13 337 ha but was extended by approximately 18000 ha in the northern part. Old boundary fences were still in place for the duration of the study while the newly acquired land (previously farmland) had been left to restore. Suikerbosrand Nature Reserve (hereafter referred to as Suikerbosrand NR), is situated at an altitude of between 1550m and 1917m above sea level (Falls 1993). The reserve falls into the summer rainfall region and experiences seasonal changes in minimum and maximum temperature and rainfall levels (Falls 1993, Figure 2.1). Annually, Suikerbosrand NR receives 705mm rainfall on average and average temperature ranges between 10-29˚C in summer and 3-24˚C in winter (data from 2000-2006; GDACE 2006). The reserve has a number of permanent water sources, including windmills, dams, springs, and seasonal rivers; the largest water body is the Sedaven Dam, situated in the south east of the reserve. Other permanent water sources have been placed in areas classified as 'sour veld' in order to prevent overgrazing of preferred grass species or 'sweet veld' (tourist map, GDACE 2006). Baboons were also observed drinking from ponds situated in the tourist campsite within the reserve and farm dams and water tanks outside the reserve.

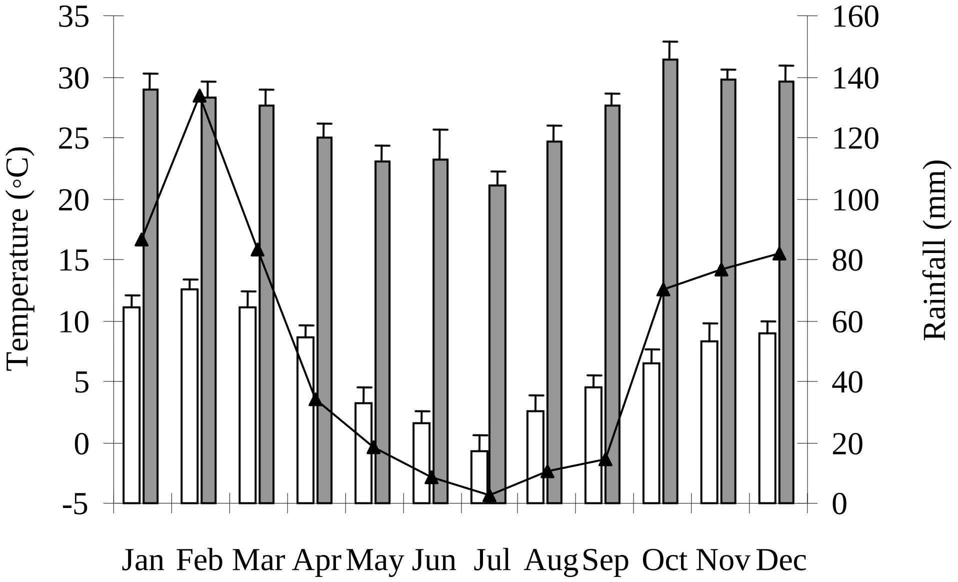

Figure 2.1 Mean (+SE) monthly temperature (minimum - white bars, maximum-grey bars) and rainfall (black line) for Suikerbosrand Nature Reserve (2000-2006, Gauteng Department of Agriculture, Conservation and Environment 2006).

Suikerbosrand is a mountainous region with a combination of grassland, *Acacia* savannah, *Aloe* forests, *Protea* veld (bush) and wooded valleys (tourist map, GDACE 2006). The vegetation in Suikerbosrand NR is described as "Bankenveld", which is classified as false grassland, characterised by sour grassland species, which have poor grazing potential, particularly in winter, and bushveld species dominant in areas with rocky outcrops and hills (Acocks 1988). The flora is diverse and grasslands contain many grass species with varying grazing potential for herbivores (Appendix).

Shrublands have numerous annual forb species and perennial shrub/bush species. Woodlands are dominated by *Acacia* and other tree species, which produce seeds, fruit and browse material seasonally.

Plant communities in Suikerbosrand NR can be divided into three general habitat types: grassland, shrubland and woodland (Figure 2.2) which is classified according to dominant and diagnostic species (Hennop pers. comm. GDACE, Table 2.1). The grassland habitat is characterised by grass and shrub species found in poor, overgrazed, or disturbed veld. Shrubland is characterised by shrub species, which provide fruit, berries and seeds but unpalatable grass species. Woodland habitat is characterised by two *Acacia* species (Table 2.1), which provide seeds, sap and browse of varying foraging potential. Grass species found in shrubland and woodland areas are indicators of average to good veld quality (Table 2.1, van Oudtshoorn 1999).

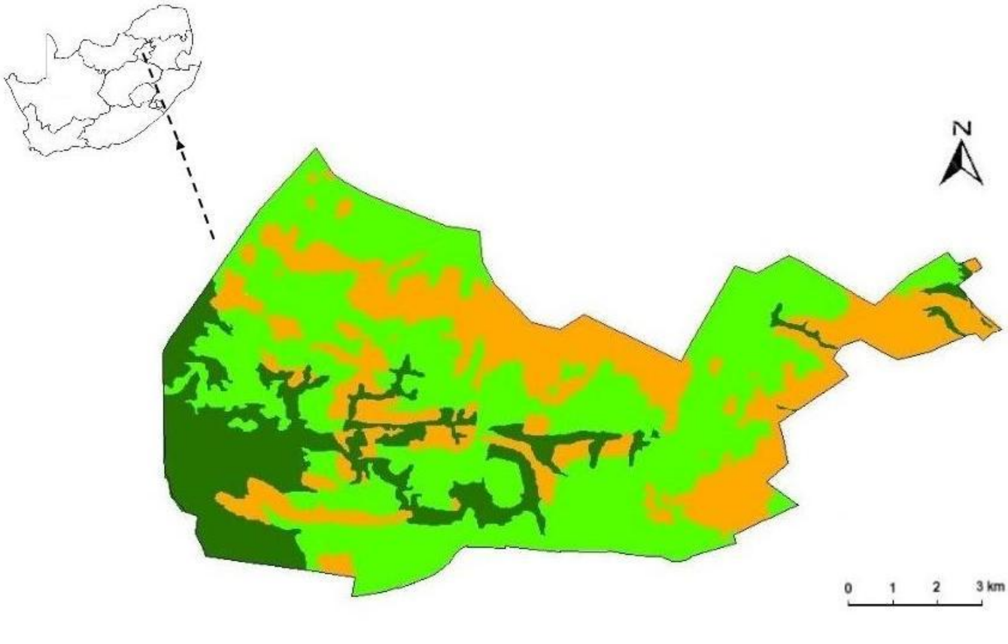

Figure 2.2 Broad habitat types found in Suikerbosrand Nature Reserve (Vegetation_Panagos 1999). Light green (grassland); orange (shrubland); dark green (woodland), inset; map of South Africa showing provincial boundaries.

Table 2.1 Categorisation of habitat type according to dominant and diagnostic plant species (Hennop pers. comm. GDACE).

Habitat type	Dominant species	Diagnostic species
Grassland	*Eragrostis plana, Setaria sphaceolata var. Sericea*	*Stoebe vulgaris, Leucosidea sericea*
Shrubland	*Hermannia grandistipula, Englerophytum magalismontanum*	*Cussinia paniculata subsp. Paniculata, Aristida transvaalensis*
Woodland	*Acacia caffra, Acacia karroo*	*Ehrharta erecta var. natalensis, Panicum maximum*

Suikerbosrand NR is contains a number of mammalian species, including herbivores, such as eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), zebra (*Equus burchelli*), black wildebeest (*Connochaetes gnou*), blesbuck (*Damaliscus dorcas phillipsi*), reedbuck (*Redunca arundinum*), mountain reedbuck (*Redunca fulvorufula*), grey rhebuck (*Pelea capreolus*), common duiker (*Sylicapra grimmia*), steenbok (*Raphicerus campestris*), springbok (*Antidorcas marsupialis*) and tsessebe (*Damaliscus lunatus*). Other mammal species include porcupine (*Hystrix africaeaustralis*), black-backed jackal (*Canis mesomelas*), genet (*Genetta genetta*), aardvark (*Orycteropus afer*), meerkat (*Suricata suricatta*), yellow (*Cynictis penicillata*) and slender (*Galerella sanguine*) mongoose, cape hare (*Lepus capensis*) and a number of small rodent species. Predators such as brown hyena (*Hyaena bruunnea*) and leopard (*Panthera pardus*) have been known to be inhabitants in this region, but are rarely sighted.

Suikerbosrand NR comprises of two geological super groups: Ventersdorp to the west, covering approximately 70% of the reserve, and Witwatersrand in the east (Falls 1993). The Ventersdorp type soils are more fertile than the Witwatersrand type and therefore offer better grazing for large mammals (Falls 1993). The topographical features of the reserve are ideal for baboons with year round availability of water, numerous available sleeping sites, and diverse vegetation and habitat types (Falls 1993).

Different types of farming activities occur adjacent to the Suikerbosrand NR. Maize and cattle (dairy) farming occur to the south of the reserve, vegetables are grown on farms to the northern and western side, and game, chicken and sunflower farming are scattered throughout adjacent farms (Hennop pers. comm. GDACE).

Harvesting time for maize can occur from the end of March until mid July but varies depending on whether planting time coincides with rainfall patterns (Hawkins pers. comm. Grain South Africa).

2.1.3 Cellular collars

Between June and November 2005, one adult female from each of the 12 known troops was fitted with a cellular collar by staff of the GDACE and Suikerbosrand NR. The collars were purchased from Animal Africa Tracking (www.awt.co.za). Due to malfunctions in two of the collars, data for only 10 troops were used in the study. Details for the 10 troops, including troop name, collar ID number and size (based on a census in 2006), are given in Table 2.2.

Table 2.2 Outline of study population, troop name, cellular collar identification and average troop size

Troop Name	**Collar ID number**	**Troop size**
Diepkloof	AS33	29
Sedaven	AS35	24
Raymond-noppe	AS36	51
Kareekloof	AS39	46
Blesbok	AS41	54
Holhoek	AS42	20
Vaalkop	AS43	68
Steenbok	AS44	50
Toringkop	AS45	37
Schoongezicht	AS55	52

The cellular collars used a Hawk105 (GPS - GSM) device which calculated the XY coordinates (longitude and latitude in decimal degrees), external body temperature, and travel speed (m/s), all of which were sent via a short message service (SMS) to a GSM network (Haupt pers. comm. Animal Africa Tracking). Initial information provided indicated that the battery life of a cellular collar was 12-months, which meant that the first collars were expected to stop broadcasting from approximately early 2007 (Hennop pers. comm. Gauteng Department of Agriculture, Conservation and Environment). However, information received from Animal Africa Tracking revealed that the collar had a battery life of 18 months and would stop broadcasting during mid 2007. Collar readings were taken at five set times, varying for each troop. Set times were chosen either by a coordinator at Suikerbosrand NR or from Animal Africa Tracking centre. These times included 3am; 5am; 7am; 9am; 11am and/or 2pm. If a troop was out of cellular coverage, readings were stored in a data logger and later sent via SMS to the network when the troops came back into cellular range. The data set used in my study represents 12 months (April 2006 – March 2007) of sampling from collars. GPS coordinates were accessed with permission from Animal Africa Tracking via their website www.yrless.com.

2.1.4 Study Population

Baboons have existed naturally in the Suikerbosrand NR area, and have become isolated from other populations over the past 100 years; the nearest known population of baboons is located in Magaliesberg, approximately 150km away (Falls 1993). Since the proclamation of the reserve in 1972, the baboon population has continued to increase from approximately 300 individuals in 1974 to 400 individuals in 1978, and 600 individuals in 1993 (Anderson 1981, Falls 1993).

Management of Suikerbosrand NR in 2006 undertook a population census, where cellular collars were used to assist in the location and identification of troops. In addition to 10 collared troops, one un-collared and eight sub-troops were counted and their GPS positions recorded. The final population size was estimated at 771 individuals. This increase has been attributed to the lack of natural predators, although leopards (*Panthera pardus*) have been known to occur in the vicinity of Suikerbosrand NR (Falls 1993).

Troops were identified by their collar identity and location within the reserve (Table 2.2 and Figure 2.3). They were distributed throughout the reserve (Figure 2.3): three troops in the northern parts (Diepkloof – AS33, Blesbok – AS45 and Toringkop – AS41); two troops in the eastern parts (Sedaven – AS35 and Steenkop – AS44); two troops in the southern parts (Holhoek – AS42 and Raymond-noppe – AS36); three troops in the western parts (Kareekloof – AS39, Vaalkop – AS43 and Schoongezicht – AS55).

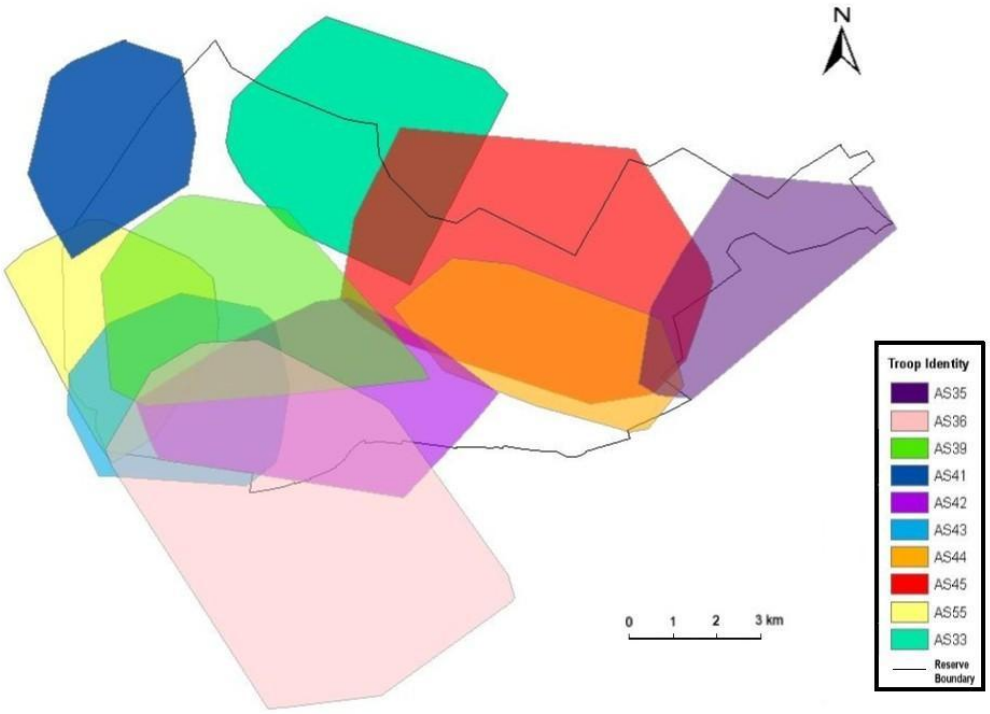

Figure 2.3 Distribution of baboon troops within and around the old boundaries of Suikerbosrand Nature Reserve.

2.2 Dung analysis

This section of the study refers to the first aim (section 1.8) which assesses the diet of troops in different areas of Suikerbosrand NR and in different seasons.

2.2.1 Collection

Dung samples were collected in order to determine the main components of the diet of the baboons over the course of the study. Dung was collected after behavioural sampling (section 2.3.1) - on the road while searching for troops, and/or when the sleeping site of a troop was located. Dung size ranged from large ±150mm, to medium ±80mm and to small ±40mm. Dung samples were collected over an area of $10m^2$, when more than one scat was present over an area of 40m, one sample was collected randomly to reduce pseudo replication. Each dung sample was placed in a plastic Ziploc™ and relevant information, such as date and time collected, locality and troop identity, was recorded. Dung was collected only when fresh, as indicated by a soft, moist consistency outside and a yellow/green to light brown colour inside. Dung was not collected if the outside and/or inside were hard and the colour was dark brown. Troop identity for dung samples was established by cross-referencing GPS points from collar information. If no corresponding troop was found, the sample was discarded.

A total of 115 different dung samples were collected from ten troops, representing a sampling effort of approximately 60% (i.e. the percentage of time that baboon dung was found in relation to the number of attempts to locate them). Two troops from which less than five samples collected were removed from the analysis, resulting in a final total of 94 samples for data analyses. The number of samples collected per troop was not evenly distributed (Diepkloof – 11 samples, Kareekloof – 8, Blesbok – 10, Holhoek – 17, Vaalkop – 11, Steenbok – 9, Toringkop – 12 and Schoongezicht – 16).

2.2.2 Sample analysis

Dung was stored at -15˚C at the University of the Witwatersrand until analysis. Thereafter, the dung was removed from the freezer and thawed for approximately 20 minutes. Each sample was divided into a third of the original portion, in order to account for the range of scat sizes collected. Each sample was then soaked in 50% ethanol for approximately 24 hours (Kerley 1992, Neal 1991, Perrin and Swanepoel 1987), placed in a Petri dish and left to dry for approximately 48 hours in a fume cupboard. The dried dung was examined under a dissecting microscope (15X magnification).

When viewing the sample under the microscope, dried material was dissected out to identify the different food types (leaf and stem; fruit and seed; invertebrate; maize) and other components (Table 2.3). Material was dissected from the midpoint of the Petri dish outwards towards the edges. The Petri dish was rotated anticlockwise so as not to repeat previously dissected areas. During initial examination, the presence or absence of each food type was determined. If only one food type was present, it would have contributed 100% but this never occurred.

Table 2.3 Description of identifying characteristics of food types and non-nutritional components used in analysis of the dung of baboons at Suikerbosrand NR.

Food type	Characteristics
Root, stem and leaf	Material in this category varies considerably. Colour can be green but is usually yellow or brown. Leaf and grass may appear undigested and retain qualities of live material, namely shape, texture and in some cases colour. Stems are woody or pulpy, and the colour ranges from light brown to almost white. Roots include all underground plant structures, including bulbs and corms. These range in texture from woody or pulpy to a mix of wire-like or hair-like fibres. It is usually light in colour.
Fruit and seed	Most seeds appear unchanged but on occasion seeds may be damaged, often split open. Pieces of seed coat are very hard and can be recognised by their grainy texture and usually have sharp edges. Colours include brown (dark to light), yellow and orange (in some cases close to red). Seeds come in many shapes and sizes, for example, round; bean-shaped; elliptical. Size range is 5 – 200mm. Fruit is recognisable by the skin, ranging from glossy to matt in texture. Berries, and occasionally fleshy fruit, remain unchanged, making the pulp and flesh of the fruit clearly distinguishable and may appear sugary or crystalline.
Invertebrate	Most small invertebrates remain unchanged, allowing for easy identification. Portions of chitinous exoskeleton are clearly distinguishable and tend to be glossy in appearance and less flexible, thus more brittle than plant material. In some instances, exoskeleton may have minute hairs or be pitted. Colours include red-brownish, florescent green or purple, or clear in the case of wings.
Maize	Maize has a characteristic white colour, but colour can vary from white to a light yellow. It tends to be hard and has an almost powdery state when broken up. The husk has a distinctive scratchy texture and is slightly translucent.
Other	Material in this category included items that did not fit into the above categories. Nutritional material included hair, feathers, eggshells, sap or gum. Non-nutritional material included stones, sand, and pieces of plastic packet or unrecognisable items.

To obtain a percentage for each food type and other components present in each sample, a scan was done to determine whether the digested material covered more or less than half of the Petri dish surface (50%, Table 2.4). If it covered more, the next question was whether percentage cover was more or less than 60% and so on. If it was less than 50%, an estimation of whether the component was more, less or equal to 40%, and so on. The percentage for some food types (i.e. invertebrates or maize) was also estimated using the procedure mentioned but percentages were characteristically low and categories of 10-15% or 1-5% was used (Hill *et al.* 2005, Kent and Coker 1996).

Table 2.4 Percentage estimation using deductive questions method to evaluate dung composition per sample.

Step	**Deductive questions**			
A	**Are all food types present?**			
i	Yes	**Step 2**		
	No	Ii		
ii	**How many food types are present?**			
	1	100%		
	between 2-4	**Step 2**		
B	**How much does each food type contribute to the overall sample?**			
i	%	Yes	No	
Q1	≥50	Step 2ii	1-50%	go to Q2
Q2	≥40	40-45	0-35	go to Q3
Q3	≥30	30-35	0-25	go to Q4
Q4	≥20	20-25	0-15	go to Q5
Q5	≥10	10-15%	1-5%	
ii	**How much does it contribute?**			
	%			
	$50 \geq X \leq 60$			
	$60 > X \leq 70$			
	$70 > X \leq 80$			
	$80 > X \leq 95$			
	$95 > X < 100$			
	Note: return to step 2i for all remaining food types			

Dung components data were calculated in proportions, so the data set were arcsine transformed to approximate normality before statistical analyses could be applied. Months were assigned to one of three seasons (after Neal 1991): dry season from May to August; early rain season from September to December; late rain season from January to April. Because of the sampling of the same troops in different seasons, the statistical analyses conformed to a repeated measures design. However, samples were not evenly spread over the months or troops, and therefore repeated measures analysis could not be used. Instead, a general linear model (GLM) was used to analyze whether troop or season (independent factors) influenced the proportion of food types and other components in the diet. Statistical analyses were performed using Statistica 6.0 for Windows (StatSoft 2001). Differences were considered significant if $\alpha \leq 0.05$. Tukey HSD post-hoc tests were used to detect specific differences among the independent variables.

2.3 Foraging Behaviour

This section of the study pertains to Aims 2 and 3 (section 1.8) which investigated individual foraging behaviour of chacma baboons in different areas of Suikerbosrand NR and assessed seasonal variation in foraging effort.

2.3.1 Data collection

Behavioural data was collected from ten troops for seven days per month from April 2006 – March 2007. All tracking and sampling was done from a car, since baboons in Suikerbosrand NR were wary of people on foot. Troops were located using GPS coordinates from the Animal Africa Tracking website. The coordinates were updated twice daily during field trips and entered into a handheld GPS (Garmin™ eTrex Summit). In addition, troops were spotted opportunistically while driving around the reserve using knowledge of the troop locality (Figure 2.3, Section 2.1.4). When a troop was located, its position was recorded using a handheld GPS and troop identity was confirmed with GPS readings from cellular collars later. Search success was approximately 40% (i.e. the percentage of time that baboons were found in relation to the number of attempts to locate them).

Behavioural observations were made only when a troop was within the boundaries of the Suikerbosrand NR, since permission was not given to enter neighbouring farms. Searching for and sampling of troops took place twice daily - approximately 7:30-12:30 and 14:00–18:00, depending on seasonal differences in the timing of sunrise and sunset.

When a troop was located, a scan of the area was conducted in order to locate members of the troop and the direction of movement of the troop. I positioned myself so that I could observe the majority of the troop for the longest time possible. Information, such as date, time, coordinates was noted and troop identity was recorded later.

Observations were made directly if baboons were less than 20m away or by using Minolta Classic 10X50 binoculars when baboons were more than 20m away. Troops were not sampled when they were more than 200m away because of difficulties observing specific behaviours (see below). Each troop was sampled for 60 minutes or for as long as the baboons were visible. A troop was only sampled if ten or more individuals were visible per 60 second interval. If less than ten individuals were observed consistently for a minimum of five focal intervals (e.g. five minutes), the observation was ended).

During observations, I recorded the behaviour of focal individuals – with an inter-focal interval of 60 seconds. To keep track of time, a tape recording was made of me marking time in 60-second intervals and played back during observations. One-zero sampling was applied to a randomly selected individual from the troop (Martin and Bateson 1986). Focal individuals were selected according to visibility and activity level (active individual chosen over inactive individual). In general, individuals were chosen in open habitats (grassland and shrubland) more than closed habitats (woodland); adults and sub-adults were chosen more often than juveniles or infants. Males and females were chosen as equally as possible; individuals were not repeated in successive sampling time interval but may have been repeated during an observation.

Focal sampling focused on foraging behaviour, which was broken down into its components – search (active or stationary scanning of the immediate area), manipulate (process food item before consumption e.g. dig, clean, peel, turn over rock) and consume (food item is placed in mouth).

2.3.2 Data analysis

A total of 83 focal samples and 32 hours of behavioural observations were collected over 12 months. The data were not evenly spread over the months and among the troops (Diepkloof – 17 samples, Sedaven – 4, Raymond-noppe – 2, Kareekloof – 8, Blesbok – 12, Holhoek - 9, Vaalkop – 8, Steenbok – 9, Toringkop – 7, Schoongezicht – 7), largely because of the unpredictable nature of locating all troops equally throughout the year (Table 2.5). The total number of occurrences per behaviour (search, manipulate, consume) was counted per sample. The total number of counts could not exceed the observation length time, e.g. in a one minute observation, an individual could have searched for food on three separate occasions, but in the analysis this would be counted only once because of the constraints of 1/0 scoring method (Martin and Bateson 1986). In order to compare behaviours from different samples, counts were converted into proportions as observation length varied for samples. For example, if an individual consumed food 10 times in a 30 minutes sample, a proportion of 0.33 was recorded. The data set were then arcsine transformed to approximate normality before statistical analyses could be applied.

Months were grouped into seasons (see section 2.2.2). Statistical analyses were performed using Statistica 6.0 for Windows (StatSoft 2001). Because of the sampling of the same troops across seasons, the statistical analyses conformed to a repeated measures design. However, since data for individual troops was not equally or consistently sampled over the three seasons, a General Linear Mixed Model (GLMM) analysis was employed, in which season was the fixed factor, troop was the random factor, and the three foraging behaviours were the dependent variables.

Observation length was included as covariate to account for proportions being underestimated in samples with longer observation lengths or overestimated in samples with shorter observation lengths. The 95% confidence intervals (post-hoc) were examined graphically to assess specific differences between independent factors when $\alpha \leq 0.05$.

Table 2.5 Summary of the number of minutes a troop was sampled per month and per season.

Troop/ Month	Diepkloof	Sedaven	Raymond-noppe	Kareekloof	Blesbok	Holhoek	Vaalkop	Steenbok	Toringkop	Schoongezicht	Total minutes	
May				46			38			30	114	**Dry season 424**
June	30	10	15		40		53		66		214	
July	14				13					15	42	
August	36					10				8	54	
September	78				41		34	30	22		205	**Early rain season 816**
October	56			34	57	9		57	6	7	226	
November	10			8	59	26	30	88	25	8	254	
December	14		36	15	41	7				18	131	
January	42				11	88				10	151	**Late rain season 698**
February	49	16		60	21	27	30				203	
March	45	50		60				20	11		186	
April	55			20	23		60				158	
Total minutes	429	76	51	243	306	167	245	195	130	96	**1938**	

2.4 Space use

The following section pertains to Aims 3 and 4 (section 1.8) which investigated seasonal and spatial patterns of foraging behaviour and effort.

2.4.1 Global information system (GIS) collection and analysis

Location (GPS) data for 10 troops was used to calculate the average distances travelled, home range size and habitat use over 12 months. All GIS analyses were conducted using the software ArcMap9 (ESRI 2004). Data from cellular collars were stored and accessed from an internet site (www.yrless.com). Data for each troop per month were downloaded and saved in a comma-delimited file (hereafter referred to as CSV). As CSV files contain XY information such as longitude and latitude, they could be imported into ArcMap9 and converted into spatial data. In order for data from CSV files to be viewed as locality points on a projected map of Suikerbosrand NR, CSV files needed to be projected onto the same coordinates system (ESRI 2004). *World geodetic system* 1984 or WGS_1984, a commonly used Geographic Coordinate System (GCS) used for locational measurements worldwide - match the Suikerbosrand NR map projection (ESRI 2004). In order to calculate information such as distances or area projected, CSV files were converted into shape files.

Because Geographic Coordinate Systems are defined according to the three dimensional spherical surface of the earth, units are angular and XY information (i.e. longitude and latitude) are measured in decimal degrees (ESRI 2004). In order to calculate distances travelled as lengths in metres and home range area in square kilometres, shape-files required a new projected coordinate system to be defined. Using the batch projection tool in Arc Toolbox, the new projected coordinate system was created as WGS_1984 (coordinate system); Suikerbos (new projection name); Transverse Mercator (projection type); central meridian 28.0000 (central point locality); scale factor of 1.00 (accuracy of measurements).

2.4.2 Distance travelled

2.4.2.1 GIS analysis

Using shape-files created in Section 2.4.1, distance travelled was analysed using Hawth's Analysis Tools© (Beyer 2004) in ArcMap9. Locality points were converted into paths per day and saved as new shapefiles for each troop per month. Lengths were calculated by adding the distance between all positions recorded per day, beginning with the first position and ending with the last position recorded for that day. An additional length field was added to the attribute table for shape-file. Using the field calculator, lengths for each path per day were calculated as:

```
Dim dblLength as double
Dim pCurve as ICurve
Set pCurve = [shape]
dblLength = pCurve.Length
```

2.4.2.2 Statistical analysis

Each month had between 28 – 31 daily distances, which were then added to provide the total distance travelled per month per troop. For troops where cellular coverage was inconsistent for more than two consecutive months, the troops were excluded from analysis. A means substitution was performed in troops where coverage in a single month was inconsistent (Zar 1999). Eight troops were used in the final analysis of distance travelled.

Because of the sampling of the same months across seasons, a GLM repeated measure design was used to analyse total distance travelled (kilometre) over 12 months. In order to gauge the influence of extraneous variables on distance travelled, mean troop size (information regarding troop size was obtained from census data and considered to be a fixed variable) and overall troop type (open, savannah and mix, section 2.4.4.1) were included as covariates in the analysis. Differences were considered significant if $\alpha < 0.05$. Tukey HSD tests were used to assess where differences occurred among troops. Due to the small sample size, season could not be used directly as an independent variable; instead, months were used in the analysis. Using the information provided by post-hocs, months were grouped into seasons to give an overall pattern.

Since none of the troops were replicated, troop could not be included as an independent variable in the analysis. Instead, chi-squared tests (InStat version 3.0; GraphPad software (2003) was used to compare differences in distance travelled between troops. Differences were considered significant if $\alpha \leq 0.05$.

2.4.3 Home range

2.4.3.1 GIS analysis

Home range size was calculated using the minimum convex polygon method, which is a widely used method in studies of movement patterns in mammals (Aebischer *et al.* 1993, Cameron 1995, Kenward 1987, Schradin and Pillay 2005). Using the minimum convex polygon function in Hawth's Analysis Tools (Beyer 2004) in ArcMap9, monthly shape-files for 10 troops over 12 months were converted into monthly home range shape-files. The minimum convex polygon tool automatically calculates area (km^2) which was added to the area field in the attributes table. Area was calculated as:

```
Dim dblArea as double
Dim pArea as IArea
Set pArea = [shape]
dblArea = pArea.area
```

Troops for which there were more than two consecutive months of inconsistent data were excluded from analysis. Nine troops were included in the final analysis (one troop was removed because only six months of data was collected).

2.4.3.2 Statistical analysis

A repeated measures GLM was used to analyse changes in home range size (km^2) over 12 months. In order to gauge the influence of extraneous variables on home range size, mean troop size and troop type (section 2.4.4.1) were included as covariates. Differences were considered significant if $\alpha \leq 0.05$. Tukey HSD tests were used to assess where differences occurred. Troop was not included as an independent variable for reasons described in section 2.4.4.2, and instead chi-square tests (InStat version 3.0) were used to analyse differences in home range size between troops. Differences were considered significant if $\alpha < 0.05$.

2.4.4 Habitat Use

2.4.4.1 GIS analysis, habitat and troop classification

Habitat use was analysed using Hawth's Analysis Tools© (Beyer 2004) in ArcMap9 using the monthly shapefiles per troop over 12 months. The animal movement tool counts the number of hits (location points) per field in a polygon shapefile. In this case, hits were counted as the number of times a troop occurred per habitat type: grassland, shrubland and woodland (Section 2.1.2, Table 2.1) from the vegetation map of Suikerbosrand Nature Reserve (polygon shape file-Vegetation_Panagos 1999, Figure 2.2).

Ten troops were used to analyse habitat use. Troops could not be analysed collectively as certain troops did not occur in all habitats; therefore, overall yearly habitat use was calculated per troop as:

$$\sum \text{hits per habitat} \Big/ \sum \text{hits all habitats} \qquad (1)$$

Troops were then divided into three troop types according to the proportion of habitat use in each habitat. Open troops (Diepkloof, Sedaven, Blesbok and Toringkop) were characterised as having > 50% habitat use in shrubland. Savannah troops (Vaalkop and Schoongezicht) were characterised as having > 50% habitat use in woodland. Mixed troops (Raymond-noppe, Kareekloof, Holhoek and Steenbok) were characterised as having < 50% habitat use in each of grassland, shrubland and woodland.

2.4.4.2 Statistical analysis

Only nine troops were used in the final analysis as one troop was not sampled in all seasons. Monthly habitat use was calculated using formula (1). Proportions were arcsine transformed before statistical analysis. As habitat type and season were repeated in each troop type, a repeated measures GLM was used to analyse habitat use for each troop type (open, savannah and mix). Differences were considered significant if $\alpha \leq 0.05$. Tukey HSD post-hoc tests were used to assess where differences occurred.

2.4.5 Line transects

2.4.5.1 Collection and sampling

Line transects were used to assess evidence of foraging activities by baboons in areas where they forage. Samples were collected from September 2006 – March 2007. Transects were conducted in areas where behavioural samples had been collected (Section 2.3.1) and/or where baboons had been seen foraging. Sites were sampled only when the baboons had left the area. Five parallel lines were walked per site. The starting position of the first transect was randomly selected and each subsequent transect was approximately 10m apart from the previous. Each transect was 100m long. Every 4m, a scan of the area ($1m^2$, 25 points per transects) was made and evidence of foraging activities by baboons was marked (Table 2.6).

Foraging activities not only gave an indication of the effort required to forage in an area but the types of food resources foraged in particular habitat types. All foraging activities observed (Table 2.6) required differing degrees of manipulation where some activities (e.g. digging) were more energetically costly than others (e.g. eating plant shoots). Activities such as digging or turning over rocks are evidence of tuber and/or insect foraging, while aloe, root and shoot foraging are self explanatory (Table 2.6). Digging was often observed during behavioural observations (termed manipulation) and therefore line transects can be regarded as the physical evidence of behavioural observations. However holes observed in isolation of known foraging sites may not be exclusively an activity carried out by baboons as other small mammals e.g. meerkat, mongoose and other rodent species are present in Suikerbosrand NR.

Table 2.6 Description of different foraging activities of baboons observed during line transects

Activity	Description
Dig	A hole 5 > x < 5cm deep. Shallow holes were typified as scratches, while deep holes were oval in shape. Digging was common around plant or grass clumps, between rocks or underneath a rock which had been over turned.
Turn rock	Rock, which had been physically moved out of initial position. Can vary in size from small (< 20cm high) to large (> 20cm high).
Aloe	Any part of the succulent plant (leaf, flower, seedpod, tuber, root) which has been manipulated. For example, leaf scraped with teeth, inner portion of plant removed.
Root	Base of plant (rhizome) which has been removed from the ground, remnants of roots usually present.
Shoot	Above-organs of plant (stem, leaf) show evidence of manipulation of bite marks, plant parts are removed from original plan.

2.4.5.2 Data analysis

Samples were categorised according to overall habitat type (grassland, shrubland and woodland) and season (dry, early rain and late rain). A total of 19 samples, each containing five replicates were collected. Troops were not evenly sampled over months or between seasons and therefore were not included as a variable in the analysis. The total number of occurrences for each foraging activity per sample was counted. In order to compare each foraging activity across seasons and habitats, frequencies were converted into proportions, as follows:

$$\text{number of times a foraging activity occurred} \Big/ \sum \text{all foraging activity occurrences}$$

The data set was arcsine transformed to approximate normality before statistical analyses could be applied. Because habitats were sampled across seasons, the statistical analysis most appropriate would have been a repeated measures design. However, since data for habitats was not equally or consistently sampled over the both seasons, a General Linear Mixed Model (GLMM) analysis was employed. Season and habitat type were fixed factors and the five foraging activities were the dependent variables. The 95% confidence intervals (post-hoc) were examined graphically to assess specific differences between independent factors when $\alpha \leq 0.05$.

Chapter 3: Results

3.1 Diet

In general, plant resources (root, stem, leaf and fruit and seed) contributed over 80% to overall diet in baboons (Figure 3.1). Vegetative and reproductive plant material contributed equally to overall diet, while invertebrates, maize and other foods contributed around 16% to overall diet (Figure 3.1).

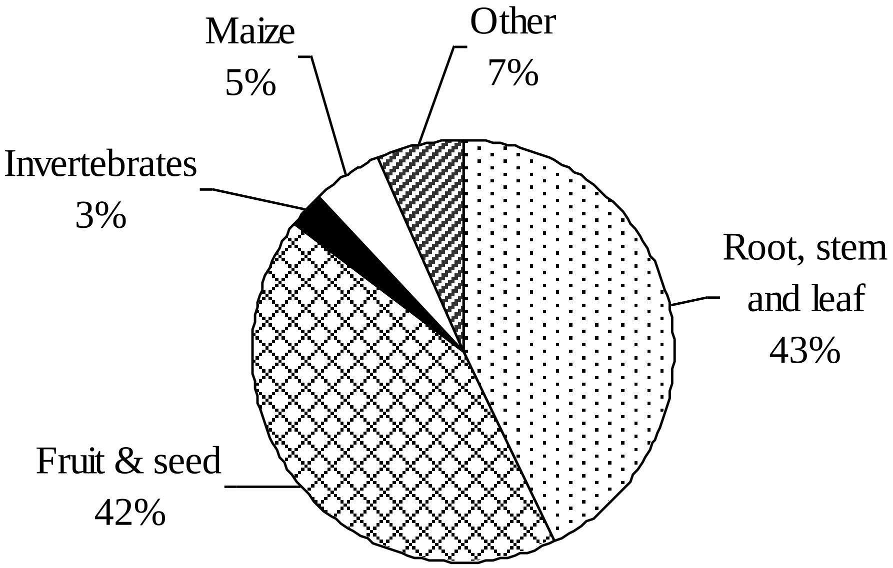

Figure 3.1 Overall food type composition in chacma baboon population in the Suikerbosrand Nature Reserve.

Dung components were significantly influenced by troop ($F_{35, 280}$=1.61, p=0.019). Tukey HSD post-hoc tests showed that troops differed in the proportion of maize consumed but not for other plant material (root, stem and leaves), fruit and seed, invertebrates or other components. The proportion of maize was significantly greater in the Holhoek troop compared to other troops, Blesbok, Vaalkop and Schoongezicht also had comparatively high proportion of maize in the dung (Figure. 3.2).

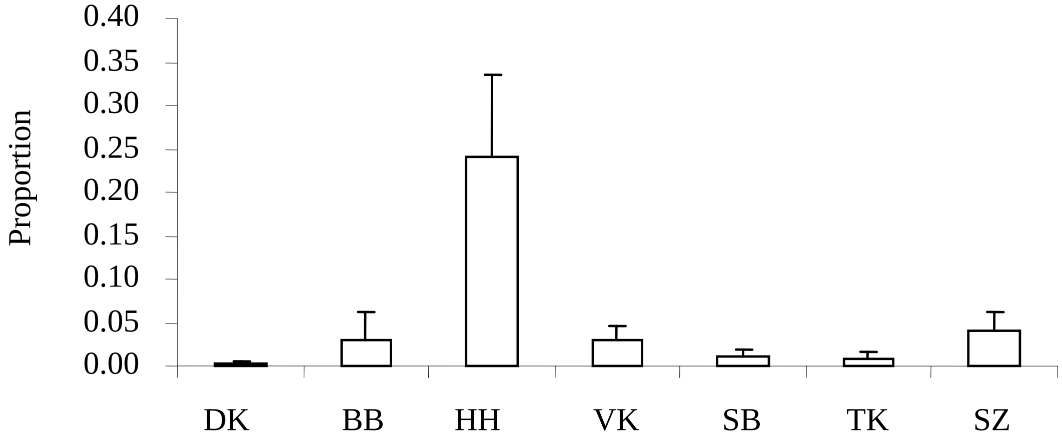

Figure 3.2 Mean (+SE) proportion of maize in diet across troops. The data of one troop (Kareekloof) were excluded, as maize was not found in the dung. Troop name abbreviations: Diepkloof (DK); Blesbok (BB); Holhoek (HH); Vaalkop (VK); Toringkop (TK) and Schoongezicht (SZ).

Season had a highly significant influence on proportion of food types in the dung ($F_{10, 132}$=5.87, $p<0.0001$). Tukey post-hoc tests showed that plant material (root, stem and leaf) was highest in the early rain season compared to the dry and late rain seasons (Figure 3.3). Fruit and seed showed a seasonal pattern opposite to that observed for the plant material, with greater proportions recorded in the dry and late rain seasons compared to the early rain season (Figure 3.3). Despite a relatively low proportion of invertebrates in the overall diet, the proportion of invertebrates consumed during the dry season was greater than in the early and late rain seasons (Figure 3.3). No seasonal trend was found in the proportion of maize in diet. The proportion of other types was greater in the dry season compared to the early rain season (Figure 3.3).

Overall, seasonal patterns in the diet suggest that when food resources are less abundant in the dry season, diet choice becomes less selective and baboons broaden their diet (Figure 3.4). When particular food types are abundant, baboons become more selective in their food choice and diet appears narrower. For example, in the early rain season, preference appears for new leaf growth as dung contained approximately 70% plant material. Similarly, over 60% of the diet in the late rain season contained fruit and seed. Root, stem, leaf, fruit and seed still contributed a large percentage of dung in the dry season but a greater proportion of other components also contributed to overall diet compared to in the early rain and late rain seasons.

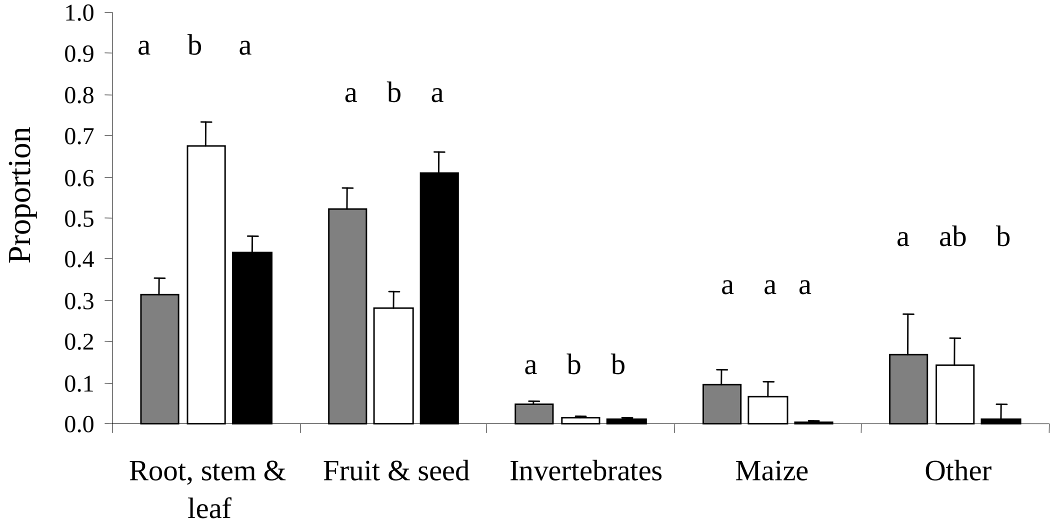

Figure 3.3 Mean (+SE) proportion of food types in the dry (grey bar, n=38), ER (white bar, n=30) and LR (black bar, n=26) seasons. Bars denoted by the same letter = not significantly different.

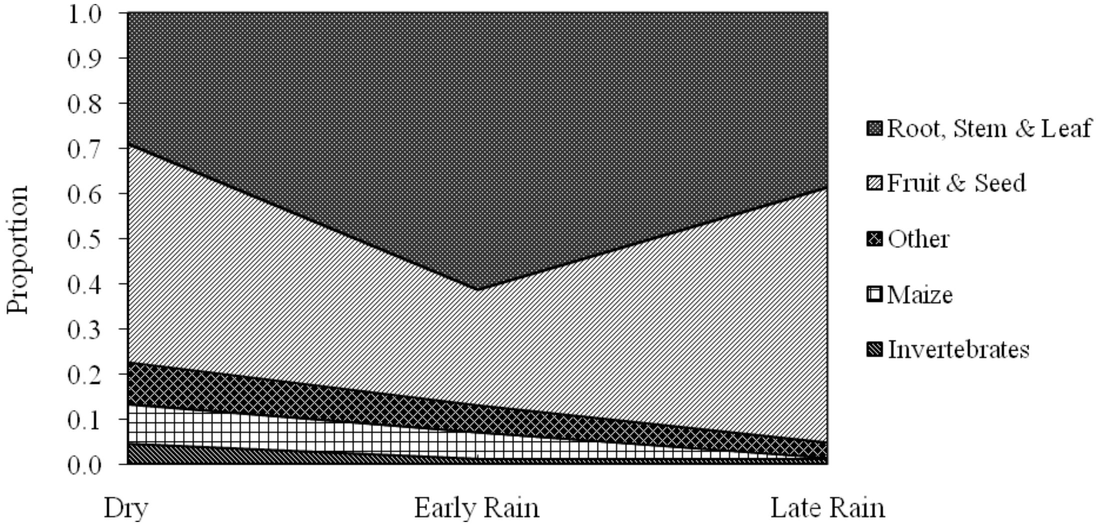

Figure 3.4 Overall proportion of food types: root, stem and leaf; fruit and seed; other; maize and invertebrate in diet over seasons.

3.2 Foraging Behaviour

Foraging behaviour showed clear seasonal patterns for all three behaviours scored (Figure 3.5). Season had a significant influence on searching behaviour, which was greater in the early and late rain seasons and lowest in the dry season ($F_{2, 64}$=5.17, p=0.008; post-hoc tests). The number of recordings of consuming behaviour was significantly influenced by season; was greatest in the early rain season, intermediate in the late rain season and lowest in the dry season ($F_{2, 62}$=3.25, p=0.045; post-hoc tests, Figure 3.1) Season also significantly influenced manipulate behaviour ($F_{2, 63}$=5.79, p=0.005). Focal individuals manipulated items more in the dry and early rain seasons compared to the late rain season (post-hoc tests, Figure 3.5). All significant results were adjusted using Bonferroni sequential adjustments, since the occurrence of behaviours was mutually dependent.

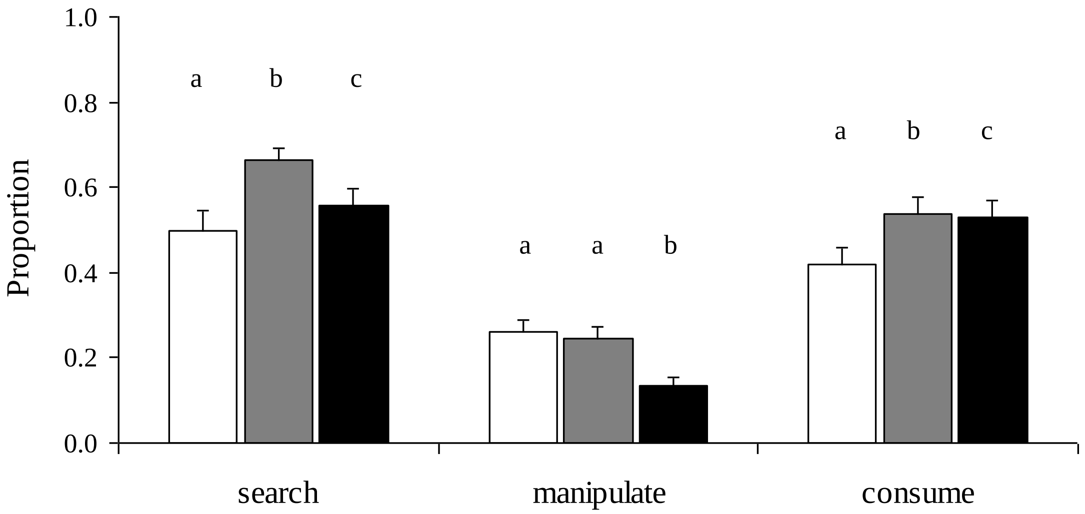

Figure 3.5 Mean (+SE) proportion of foraging behaviours - search, manipulate and consume - in the dry (white bar), early rain (grey bar) and late rain (black bar) seasons. Bars donated by the same letter = not significantly different.

Troop did not significantly influence foraging behaviours: consume ($F_{9, 55}$=0.65, p=0.749), manipulate ($F_{9, 55}$=0.13, p=0.137) or search ($F_{9, 55}$=0.43, p=0.434). Likewise, no combination between troop and season showed any influence on foraging behaviours. Observation session length (i.e. the number of minutes a sample lasted), had no influence on all three foraging behaviours: consume ($F_{1, 63}$=1.65, p=0.203), manipulate ($F_{1, 61}$=0.09, p=0.766) and search ($F_{1, 64}$=0.03, p=0.861).

3.3 Movement patterns and space use

3.3.1 Distance travelled

Due to the small sample size, season was not used directly as an independent variable; instead months were used in the analysis.

3.3.1.1 Season

Distance travelled was significantly influenced by month ($F_{11, 77}$=5.74, $p < 0.0001$). Grouping the months into seasons, post-hoc tests revealed that distance travelled in dry season months (May, June, July, August) was lower than months in the early rain (October, November, December) and late rain (January, March) seasons (Figure 3.6). Mean seasonal distance travelled in all troops was 276.6km in the dry season, 396.6km in the early rain season and 377.2km in the late rain season. Total distance travelled ranged from 36.4 – 107.4km in the dry season, 69.3 – 153.4km in the early rain season and 40.5 – 136.7km in the late rain season.

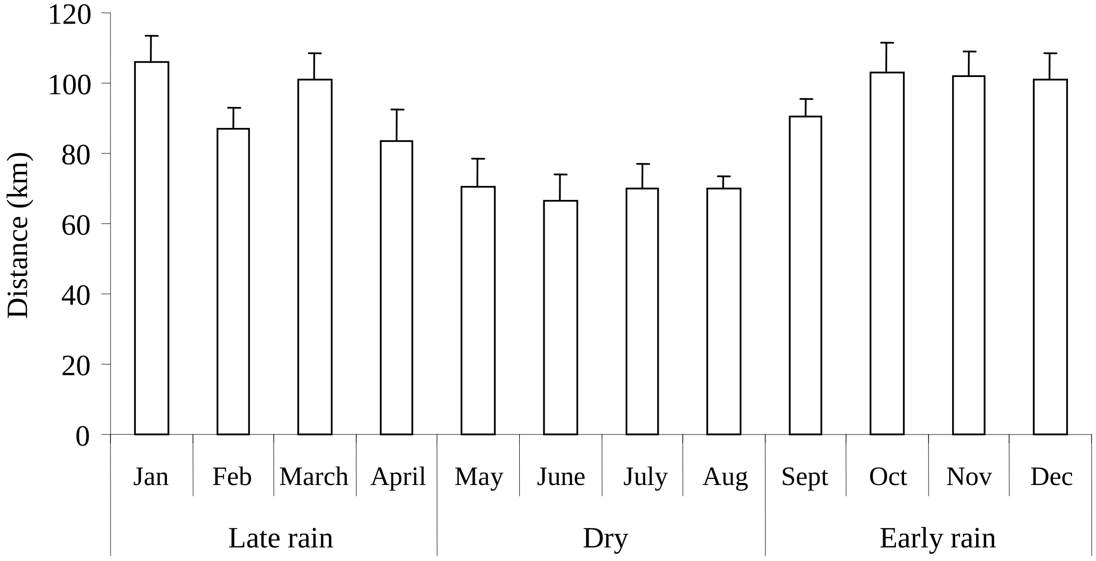

Figure 3.6 Mean distance travelled monthly (n=77). Error bars represent +SE.

When I re-analysed the same data set to include troop size and habitat as covariates, troop size had a significant effect on the overall analysis ($F_{1,5}$= 10.47, p =0.023) while habitat type showed no effect on distance travelled ($F_{1,5}$=2.599, p = 0.168). As a result, distance travelled was now not influenced by month ($F_{11,55}$= 0.58, p = 0.843) as in the first analysis, nor by any interactions of month with covariates troop size ($F_{11,55}$= 0.31, p = 0.981) or habitat interaction ($F_{11,55}$= 0.57, p = 0.84). The change in findings in the analysis with covariates is likely caused by the reduced number of degrees of freedom in an already small population size (StatSoft 2001).

3.3.1.2 Troop differences

Distance travelled was significantly different between troops over months (χ^2 =284017, df= 77, p < 0.0001) where both mean distance and the range of distances travelled by different troops varied greatly (Table 3.1). Multiple pair-wise troop comparisons showed that all troops were significantly different from one another. Mean monthly distance travelled was greater in troops Raymond-noppe, Kareekloof, Vaalkop and Toringkop than in troops Diepkloof, Sedaven, Holhoek and Schoongezicht (Table 3.1).

Table 3.1 Summary of mean (+SE) monthly distances travelled (km), minimum and maximum distance travelled (km), range and total of distance travelled (km) in troops (n=8).

Troop	Mean (SE)	minimum	maximum	Range	Total
Diepkloof	81.8 (5.6)	56.2	120.4	64.2	981.9
Sedaven	72.1 (3.0)	57.8	96.7	38.9	865.7
Raymond-noppe	100.2 (9.5)	45.5	153.5	108.0	1202.1
Kareekloof	97.3 (7.5)	39.4	128.3	89.0	1167.4
Holhoek	75.2 (7.7)	36.4	120.7	84.2	902.7
Vaalkop	95.7 (3.7)	76.1	118.3	42.2	1148.0
Toringkop	94.6 (8.5)	53.6	138.2	84.6	1134.6
Schoongezicht	83.4 (3.5)	62.7	102.4	39.7	1001.1

The range of distances travelled over months was highest in Raymond-noppe, intermediate for Diepkloof, Kareekloof, Holhoek and Toringkop and lowest in Sedaven, Vaalkop and Schoongezicht (Table 3.1). Total distance travelled in troops over 12 months ranged between 865.7 km for Sedaven and 1202.1 km for Raymond-noppe.

3.3.2 Home range size

Due to the small sample size, season could not be used directly as an independent variable, instead months were used in the analysis, and therefore months were grouped into seasons to give an overall pattern, using information provided by post-hocs.

3.3.2.1 Season

Home range size varied from the smallest recorded area of 3.7km^2 for the Holhoek troop in the dry season to the largest recorded area of 29.2 km^2 for the Raymond-noppe troop in the early rain season. Home range size was not influenced by month ($F_{11, 88} = 0.29$, $p = 0.985$), indicating that there was also no seasonal pattern in home range size (Figure 3.7). Mean home range size in the dry, early and late rain seasons was 12.6km^2, 12.6km^2 and 12.9km^2 respectively.

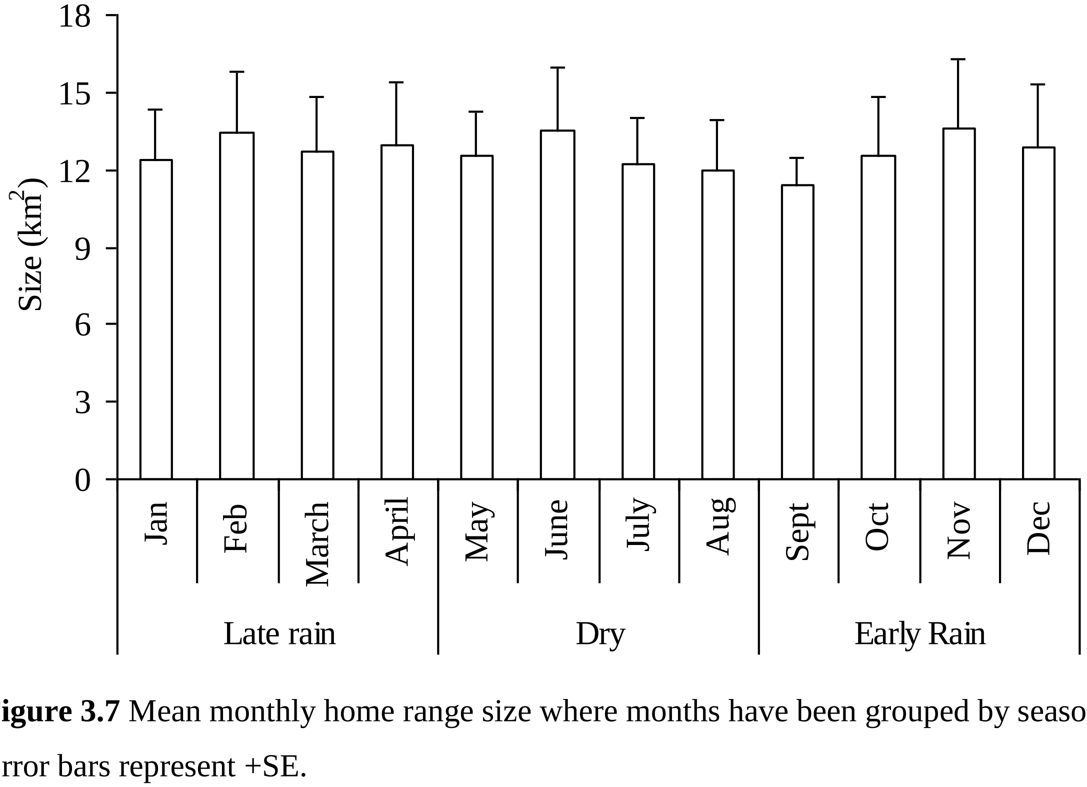

Figure 3.7 Mean monthly home range size where months have been grouped by season. Error bars represent +SE.

3.3.2.2 Troop differences

Overall mean troop home range size was 12.7km^2 with the smallest mean home range size being 8.1km^2 for Diepkloof and the largest being 22.5km^2 for Raymond-noppe. Most troop home ranges were between 8 and 12km^2. Troop did not have a significant effect on home range size (χ^2 = 82.03, df = 88, p = 0.659).

3.3.3 Habitat Use

In my analysis of habitat use, I categorised troops according to overall habitat assemblage of three broad vegetation types (grassland, shrubland and woodland) within their home range. Troops were referred to as either 'open' (mainly shrub-land vegetation available), 'savannah' (mainly woodland vegetation available) or 'mix' (all vegetation types equally available). In the results and discussion, which follow, two types of space use patterns are described: home range use (seasonal use of all vegetation types within the home range) and habitat use (seasonal use of one vegetation type within home range).

A separate analysis was conducted for habitat use for the three troop types (open, savannah and mix). The results for each troop type are reported separately below (sections 3.3.3.1 – 3.3.3.3) and then summarised in section 3.3.3.4.

3.3.3.1 Open troops

Vegetation type and season showed a highly significant effect on habitat use in open troops ($F_{8, 24}$=10.56, p<0.0001). Post-hoc tests showed that shrubland use in the dry season was greater than in the early rain and late rain seasons (Figure 3.8.a). Grassland use in the dry season was similar to woodland use in all seasons but lower when compared to grassland use in the early rain and late rain seasons. Overall, home range use was greater in shrublands (mean, 0.75) than grasslands (0.26) and woodlands (0.09).

3.3.3.2 Savannah troops

Vegetation type and season had a significant effect on habitat use in savannah troops ($F_{8, 8}$=8.28, p=0.003). Post-hoc tests showed that overall woodland use was different to shrubland use in all seasons (Figure 3.8b). While grassland use in the dry and late rain seasons were lower than woodland use, grassland use in the early rain season did not differ significantly from woodland use in all seasons (Figure 3.8.b). Habitat use in woodland differed in all seasons, being greatest in the dry season compared to the late rain and early rain season (Figure 3.8.b). Similarly, grassland use differed in all seasons, being lowest in the dry season, greatest in the early rain season and intermediate in the late rain season (Figure 3.8.b). Shrubland use was greatest in the dry season compared to late rain and early rain seasons (Figure 3.8.b).

3.3.3.3 Mix troops

Neither vegetation type nor season had an effect on habitat use for mix troops ($F_{8, 16}$=0.30, p=0.955). Habitat use in troops was evenly spread over all habitat types and troops showed no preference for any particular habitat type seasonally (Fig 3.8.c).

3.3.3.4 Overview

Patterns of home range use in troops were influenced by overall habitat occupation. For open troops, home range use was greater in the vegetation types that were more common, e.g. shrubland (Figure 3.8.a). Seasonal patterns emerged in these troops for their use of grassland vegetation, which was greatest in the early rain season and lowest in the dry season (Figure 3.8.a). A similar pattern was seen in savannah troops in both woodland and grassland habitats (Fig. 3.8.b). In addition, both open and savannah troops changed their habitat use from the rainy to the dry season: open troops mostly used shrubland (Figure 3.8.a); savannah troops mostly used woodland in the dry season (Figure 3.8.b). In contrast, mix troops (i.e. troops occupying areas with heterogeneous vegetation types), showed no clear habitat preference or seasonal pattern of habitat use (Figure 3.8.c).

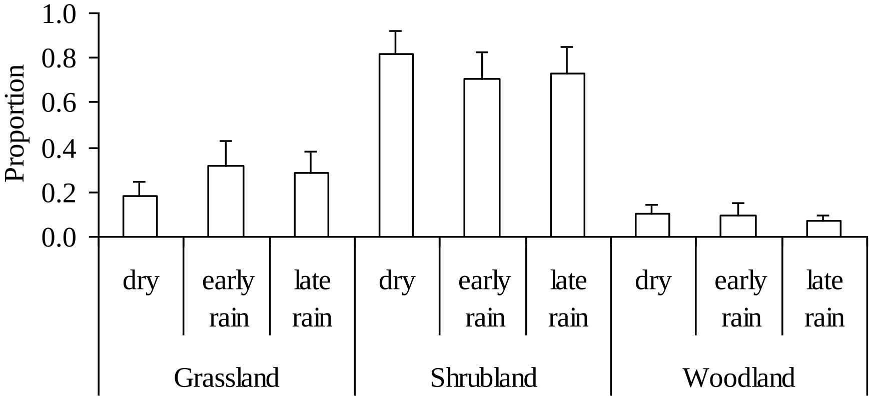

Figure 3.8.a Mean (+SE) habitat use by open troops (n=4) seasonally in the different vegetation types

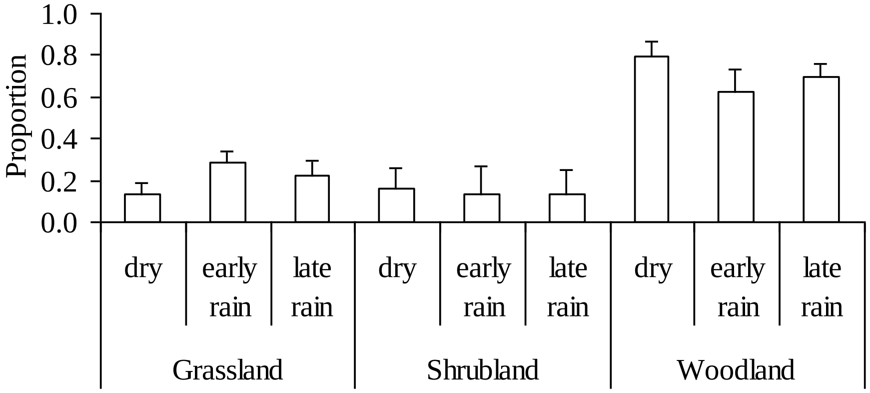

Figure 3.8.b Mean (+SE) habitat use by savannah troops (n=2) seasonally in the different vegetation types

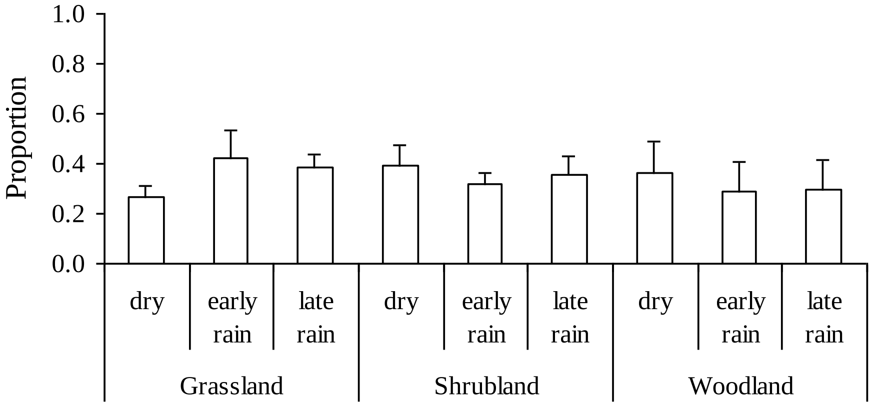

Figure 3.8.c Mean (+SE) habitat use by mix troops (n=3) seasonally in the different vegetation types

3.3.4 Line Transects

Season had a significant influence on the occurrence of rocks turned over ($F_{1,13}$=17.78, p=0.001) and roots foraged ($F_{1,13}$=9.22, p=0.009) but not on digging ($F_{1,13}$=0.001, p=0.976), foraging on plant shoots ($F_{1,13}$=2.96, p=0.109) or aloes ($F_{1,13}$=0.74, p=0.405, Figure 3.10). Post-hoc tests revealed that rock turning was greater in the late rain season (mean: 0.52) than in the early rain season (0.44) and roots were foraged more in the early rain season (0.49) than in the late rain season (0.09, Figure 3.9).

Habitat type did not influence any foraging activity: digging ($F_{2,13}$=0.06, p=0.936); rock turning ($F_{2,13}$=0.72, p=0.503); foraging for roots ($F_{2,13}$=0.18, p=0.837) plant shoots ($F_{2,13}$=0.83, p=0.459) or aloes ($F_{2,13}$=0.21, p=0.814). The occurrence of rocks turned over did show a significant habitat - season interaction ($F_{2,13}$=4.07, p=0.042). Post-hoc tests revealed that more rocks were turned over in shrubland in the late rain season compared to all other habitats in all seasons (Figure 3.10). Similarly, the occurrence of rocks turned over in grassland in the late rain season was greater than in the early rain season and compared to woodlands in both seasons and shrublands in the early rain season.

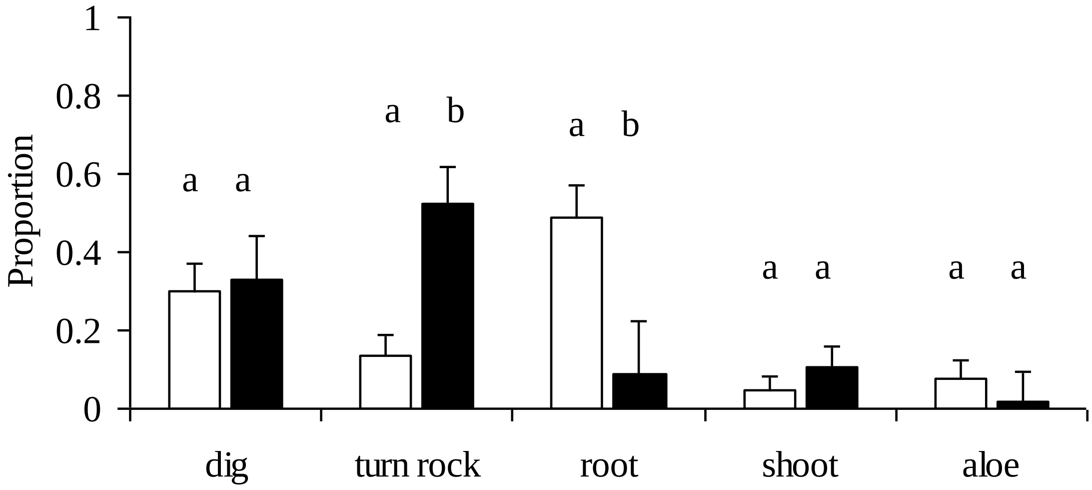

Figure 3.9 Mean proportion of foraging activities in early rain (n= 13, white bars) and late rain seasons (n= 6, black bars). Error bars represent +SE.

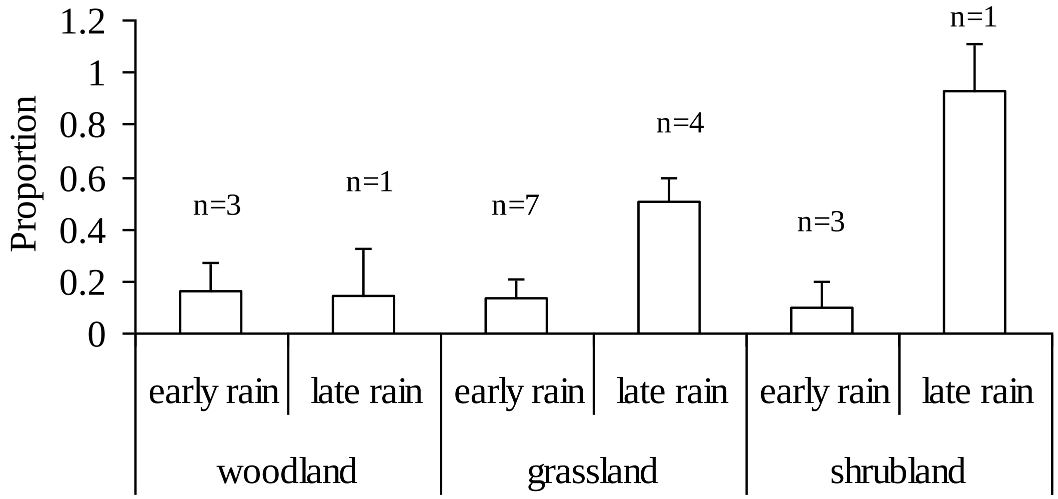

Figure 3.10 Mean proportion of rocks turned over habitats and between seasons. Error bars represent +SE

Chapter 4: Discussion

Baboon behaviour has been extensively studied in many naturally occurring populations throughout Africa e.g. yellow baboons (*Papio hamadryas cynocephalus*) in Tanzania (Altmann and Altmann 1970, Brownikowski and Altmann 1996, Post 1981, Stacey 1986, Collins 1984), olive baboons (*Papio hamadryas anubis*) in Uganda and Tanzania (Hill 2000, Barton *et al.* 1992), hamadryas baboons (*Papio hamadryas hamadryas*) in Ethiopia (Kummer 1968) and chacma baboons (*Papio hamadryas ursinus*) in southern Africa (Anderson 1981, Davidge 1978, Hamilton *et al.* 1978, Hill *et al.* 2003, Noser and Byrne 2007). Baboons are well known for their ability to modify their behaviour and diet in response to the prevailing environmental conditions (Hill and Dunbar 2002).

I investigated the foraging behaviour and diet of chacma baboons in a small, isolated mountainous grassland reserve (Suikerbosrand Nature Reserve). By studying the behaviour of several troops, I aimed to establish within and between troop seasonal variations in foraging behaviour. Since very little was known about the baboons in Suikerbosrand NR, I adopted a broad approach: studying the behaviour of troops, their space use, and diet of selected troops.

In this chapter, I discuss the findings of each of the three components of my study and then provide a simple foraging model based on the costs and benefits of foraging in a seasonal environment. I also discuss some factors, which may contribute to raiding behaviour.

Seasonal patterns in diet concurred with predictions, because when resources were less abundant in the dry season, chacma baboons broadened their diet. During the months after the initial spring rainfall, diet was dominated by plant material, while towards the end of the rainy season; diet was primarily composed of fruits and seeds. Moreover, chacma baboons in Suikerbosrand NR changed their foraging behaviour seasonally. Contrary to predictions, however, foraging behaviour did not differ among troops and home range sizes did not show seasonal or spatial differences. Stability in home range size suggests that resource availability within home ranges sufficiently meets the energy requirements of troops. My findings suggest that rather than increasing foraging effort to meet energy needs, baboons forage conservatively. Conversely, in the early and late rain seasons, baboons increase their foraging effort, most likely to exploit better foraging opportunities.

4.1 Diet

The increase in plant material in the dung collected in the early rain season corresponded with the increased primary productivity of plants following natural and managed fire occurrences and increased rainfall (Cowling *et al.* 1997). I observed that after fires in July - August 2006 burnt much of the reserve, baboons foraged on invertebrates, seeds and other foods exposed by the fire. Within weeks, the new plant (grass and forbs) shoots were consumed by both baboons and many other herbivorous mammals found in the reserve. Young plants and leaves are good sources of protein and minerals, and have low fibre, tannin and toxin levels (Altmann 1998), which may explain why baboons in Suikerbosrand NR preferred vegetative plant matter over other foods for much of the early rain season (September –November).

Invertebrate remains were present in dung collected in all seasons but were highest in the dry season. The types of invertebrate species found included termites, ants, grasshoppers and carabid beetles. Invertebrates provide a good source of fat and protein (Altmann 1998). Although the contribution of invertebrates in the diet was small, in the dry season when the food availability is lower, the additional nutritional contribution of invertebrates may be important (Lambert 1998).

Fruit and seeds from various plant species were found in the diet throughout the collection period, indicating that these food types were important sources of nourishment. Ripe fruit contains high sugar and carbohydrate levels (Kuns and Linemair 2007), while seeds provide a good source of protein and fatty acids (Heller *et al.* 2002). In addition to the findings of the dung analysis, transect sampling indicated seasonal differences in the exploitation of different food types. Fruit from the buffalo thorn tree (*Ziziphus mucrunata*) was heavily foraged by most troops, with the exception of those on the eastern side of the reserve, throughout the dry season (April through to August) and to a lesser extent at the beginning of the early rain season in September (pers. obs.). The fruit was eaten at all stages of ripeness (yellow-unripe, orange-ripe, red-over ripe); the outer fruit layer was digested but the hard inner shell protecting the seed was found undigested in the dung. In some instances, areas around *Ziziphus mucrunata* trees were littered with whole and/or cracked casings of the fruit. Chacma baboons in other localities in southern Africa also forage on buffalo thorn fruit (Hamilton *et al.* 1978, Marais 2005). Fruit and berries from other plant species were found in the diet but unfortunately these could not be identified.

Acacia trees (*Acacia karro* and *Acacia caffra*) were another important food source, and the remains of seed pods, seeds and gum (recognised by sticky substances) were found in the dung. Acacias were consumed by troops in the southern and south-western regions of the reserve. Grasses were foraged over the entire period of sampling, but different parts were consumed seasonally. Seeds and roots were recorded in dung samples during the dry season, rhizomes were eaten in the dry and early rain seasons, and leaves were eaten in the early and late rain seasons.

Many parts of the succulent *Aloe greatheadii var. davyana* were consumed in the late rain and dry seasons, including the leaf, inner storage organ, seeds, roots and tubers. Succulent plants may provide an additional source of water and nutrients during foraging (Sajeva and Constanzo 1997). Foraging on aloe plants was observed in all habitats but predominantly in troops on the western parts of the reserve, where aloes were common. Falls (1993) also observed consumption of aloes by baboons in Suikerbosrand NR. In addition, the Suikerbosrand NR baboons were reported to forage on mountain aloes (*Aloe marlothii*), by sucking nectar from flowers as well as eating the inflorescences when they were young (Symes unpublished)

Overall, the diet for Suikerbosrand NR baboon population was dominated by plants and fruits, with other food types, such as invertebrates, contributing a small proportion to the diet. In comparison to other areas in South Africa, the diversity of plant species in Suikerbosrand NR is greater, especially considering the small area which the population occupies (Anderson 1982). Similar diets were seen in previous studies in Suikerbosrand NR and in Cape of Good Hope Nature Reserve (Table 4.1). However, other populations studied in southern Africa differed in the overall diet composition. For example, some populations consume fruit (Blyde Canyon Nature Reserve - Mpumalanga, Okavango swamps - Botswana and Mkuzi Nature Reserve – KwaZulu-Natal) or underground plant organs (Giant's Castle Nature Reserve - Drakensberg, Table 4.1). All populations show similarities in the percentage of animal matter included in diet, which is low especially when compared to baboons in equatorial Africa (Whiten *et al.* 1991).

Table 4.1 Comparison of the diet of chacma baboons in five populations in South Africa and one population each in Namibia (Namib Desert) and Botswana (Okavango). Percentages of broad food categories are described as plant (leaf, tuber, and root material), fruit and seed, animal (invertebrate) and other.

Study Site / Food type	Plants	Fruit/ seeds	Animal	Other	Reference
Suikerbosrand Nature Reserve, Gauteng	43	42	3	12	present study (2006)
Suikerbosrand Nature Reserve, Gauteng	47	43	3	7	Anderson pers. comms., in Hill and Dunbar (2002)
Cape of Good Hope Nature Reserve, Cape Peninsula	41	42	3	12	Davidge (1978)
Giant's Castle Nature Reserve, Drakensberg	79	3	4	14	Whiten *et al.* (1987)
Blyde Canyon Nature Reserve, Mpumalanga	<10	>60	<10	16	Marais (2005)
Kuiseb River Canyon, Namib desert	28	72	Trace		Hamilton *et al.* (1978)
Mkuzi Nature Reserve, KwaZulu-Natal	7	90	3		Gaynor (1994)
Okavango Swamps, Botswana	16	82	<2		Hamilton *et al.* (1978)

4.2 Foraging behaviour

4.2.1 Seasonal differences in foraging behaviour

Foraging behaviour is rarely influenced by one factor alone and foraging patterns are responsive to changing environmental factors (Brownikowski and Altmann 1996, Iwamoto and Dunbar 1983, Jolly 1985). For example, day length constrained foraging activity of chacma baboons in the Cape Province, South Africa, in that fewer light hours in winter months restricted time needed to forage, travel, rest and socialise, whereas in summer, there was an increase in foraging flexibility and time allocated to other non-foraging behaviours (Hill *et al.* 2003). Changes in foraging behavioural patterns in baboon troops in Suikerbosrand NR were directly associated with seasonal variations in resource availability. In the dry season, baboons searched less for food compared to the early and late rain seasons.

Baboons were predicted to consume more food (i.e. ingest food) in the dry season when energy requirements are greatest. However, results showed that baboons consumed more in the early and late rain seasons than in the dry season, which would indicate that energy needs are greater in the rainy season and low in the dry season. However, according to Cant and Temerin (1984), harvest rate of food items in an area is influenced by the total amount of food that can be consumed by an individual. Therefore in the dry season with fewer resources available and increased time needed to access items (i.e. increased manipulation), the rate at which a baboon in Suikerbosrand NR consumed food decreased. Conversely, in the early and late rain seasons, overall harvest rate was greater due to increased food availability and less intensive manipulation required.

Similarly, Silk (1987) found that yellow baboons (*Papio hamadryas cynocephalus*) in the Amboseli National Park, spent more time foraging on specific parts of plants (e.g. tubers, grass blades and seeds) than others (e.g. fruit, gum, leaves and flowers). Furthermore, baboons spent more time foraging on grass blades, leaves and flowers during the rainy season, and less time foraging on fruit and tubers (Silk 1987). Additionally, Pochron (2005) predicted that yellow baboons (*Papio hamadyras cynocephalus*) in Ruaha National Park, Tanzania, would increase intake rate of food types, which provide higher energy gain. For example, Pochron (2005) ranked food types according to total grams consumed per minute, where fruit, flowers and seeds were ranked highest (260 – 96g/min), tubers and leaves ranked second (58-26g/min) and termites, grass seeds and meristems ranked lowest (14-3g/min).

Manipulation of food or objects (e.g. rocks) to access food is an integral aspect of the foraging behaviour in baboons, since it allows them to access otherwise inaccessible food (Barton and Whiten 1994, Hamilton *et al.* 1978, Whiten *et al.* 1987), particularly when plant resources are depleted or unpalatable. Different food types require differing degrees of manipulation: plant parts such as tubers, roots and seeds require more manipulation before consumption compared to fruit, leaves and flowers (Clymer 2006, Post 1981). In my study, baboons manipulated food material and/or objects more in the dry and early rain seasons than in the late rain season. During the dry season, baboons were observed turning over rocks (indicative of foraging for invertebrates; Estes 1992, Davidge 1978), scratching just below the surface (rhizome and seed foraging; Altmann and Altmann 1970) and in very dry areas, digging deep holes (root/tuber foraging; Whiten *et al.* 1987). In the early rain season, there was some evidence of baboons digging for and carefully selecting plant rhizomes, leaves and young stems.

Seasonal differences in foraging behaviour have been observed in other mammals. Owen-Smith (1994) proposed that during the dry season mammals' use stored body fat reserves as a physiological mechanism for coping with poor food availability and increased thermoregulatory cost. During the wet season, food intake is increased in order to recover from fat reserves depleted in the dry season, and build up fat reserves in preparation for the following dry season (King and Murphy 1985). The limited studies of the influence of thermoregulatory cost on baboon foraging behaviour suggest that baboons adjust their daily activity patterns and microhabitat use in response to thermal constraints in the environment and seasonal availability of resources (Hill *et al.* 2004).

4.2.2 Troop differences in foraging behaviour

Contrary to predictions, foraging behaviour did not differ between troops. This could be a consequence of small sample size. As the number of times each troop was sampled was not equal or equally spread throughout the data collection period, fine scale differences in foraging behaviour could not be detected. Troop difference in foraging was observed in other aspects of foraging behaviour patterns but at broader spatial scales (e.g. habitat use), which will be discussed below.

4.3 Distance travelled and foraging effort

Energy requirements vary depending on both intrinsic (e.g. thermoregulation, Iwamoto and Dunbar 1983) and extrinsic costs (e.g. environmental, Salamolard and

Weimerskirch 1993; Schwailbold and Pillay 2006). Monthly distance travelled and the proportion of time spent searching was used to assess foraging effort.

Two major hypotheses have been used to explain the relationship between primate foraging strategies and variation in seasonal patterns in resource availability. The first hypothesis predicts that animals forage more and travel further when resources are fewer and forage less and travel more when resources are abundant (Jolly 1985). The second hypothesis predicts that animals travel more in seasons when food is abundant, investing more energy into foraging, and consequently increasing energy gain under favourable conditions (Jolly 1985). When resources are scarce, animals conserve energy by travelling less and reducing energy cost of foraging (Jolly 1985, Yiming 2002).

I predicted that the foraging effort of baboons in Suikerbosrand NR would follow the first hypothesis because of the highly seasonal availability and abundance of food resources and distinct seasonal fluctuations in the climate in Suikerbosrand NR. This pattern was observed in other baboon populations (e.g. chacma baboons in the Drakensberg Mountains, Henzi *et al*. 1992, chacma baboons in the winter rainfall Cape Fynbos region, Davidge 1978, olive baboons in the Laikipia Plateau, Kenya, Barton *et al*. 1992).

However, the foraging behaviour of baboons in Suikerbosrand NR supports the second hypothesis: baboons searched less for food in the dry season when resource availability was low, whereas, in the early and late rain seasons when resource availability was high, they searched more. Equally, distance travelled was shorter in the dry season and greater in the early rain and late rain seasons. This foraging pattern has been observed in other primate species (e.g. sifakas, gibbons, and green monkeys; Jolly 1985, Harrison 1983, Raemaekers 1980), chacma baboon populations in the Cape Province, South Africa (Davidge 1978, Hill *et al.* 2003) and previously in the Suikerbosrand NR (Anderson 1982).

In a previous study of the baboons in Suikerbosrand NR, Anderson (1981) found that distance travelled was positively associated with troop size in both summer and winter. In my study, distance travelled differed between troops, but it was not possible to assess how distance travelled was influenced by troop size and habitat type. Troop size in Suikerbosrand NR ranged from 20 to 68 individuals. A pattern emerged in certain troops, where distance travelled was lower in troops with fewer members (i.e. Diepkloof, Sedaven and Holhoek) and greater in troops with more members (i.e. Vaalkop, Raymond-noppe and Kareekloof, Figure 4.1).

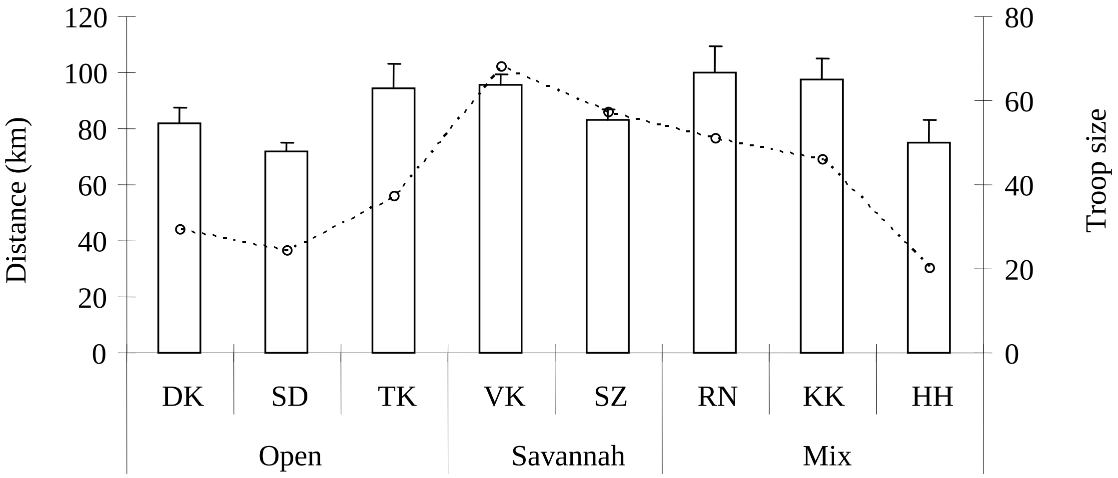

Figure 4.1 The relationship between mean distance travelled by troops (n=8) and troop size and habitat type. Error bars represent +SE

However, factors such as habitat type and quality within home range may influence distance travelled and consequently foraging effort, creating confounding patterns in comparing distance travelled among troops (Barton *et al.* 1992, Marais 2005). For example, distance travelled differed in similar sized troops found in different habitats i.e. distance travelled in troops found in mixed habitats (Kareekloof and Raymond-noppe) was greater than in a troop found in savannah habitat (Schoongezicht, Figure 4.1). In addition, distance travelled in a larger troop (Vaalkop), found in savannah habitats was similar to a smaller troop (Toringkop), found in open habitats (Figure 4.1).

4.4 Social foraging and fission-fusion behaviour

Mean troop size in Suikerbosrand NR has decreased (Table 4.2) from 78 individuals (Anderson 1981) to 48 individuals in my study. This is consistent with the finding that mean troop size often declines with increasing population density (Horiuchi 2006).

Table 4.2 Overview of previous and current population sizes, estimated population density, occurrence of sub-trooping and approximate troop size

Year of census	Number of troops counted	Home range location	Population size (Falls, 1993)	Density (population size/ 133.37 km^2)	Occurrence of sub-trooping	Average troop size
1974	7	entire reserve	299	2.2	no	43
1976	5	central, north west, east	277	2.1	no	55
1978	4	central, north west, south west and south	460	3.2	yes	78
1993	7	entire reserve	622	4.7	yes	61
2006	12	entire reserve	771	5.8	yes	48

In Suikerbosrand NR, Anderson (1981) found the occurrence of smaller sub-troops was greater during winter and spring than in the summer and autumn. Fission-fusion or sub-trooping behaviour is a mechanism of coping with seasonal pressures on food limitations by lowering foraging costs and decreasing intra-troop competition (Anderson 1989), where smaller foraging parties' lower energy expenditure by decreasing distance travelled and foraging time.

The benefits of flexible sub-trooping behaviour in a population such as the one found in Suikerbosrand NR, is that social family units such as troops can respond to changes in the environment over short time scales (Chapman and Chapman 2000, Lehman *et al.* 2007). This is especially relevant in the dry season when minimum temperatures may drop well below 0˚C and food availability is most limited. In the summer months, sub-troops rejoin larger family groups, which may be related to more mating opportunities (Anderson 1989) and better success at locating clumped food resources when the cost of competition for food is lower (Beauchamp 2007, Sontag *et al.* 2006). Recent population censuses by Falls (1993) and GDACE (2006) confirm that sub-trooping behaviour is still present within the population (Table 4.2). However, sub-trooping was not directly noted during my study.

A benefit of foraging in a large troop is increased vigilance against predators (Cowlishaw 1997). However, predators which actively hunt baboons (e.g. leopard, *Panthera pardus*) have been absent in Suikerbosrand NR for many years (Anderson 1981, Falls 1993). Other predator species found in Suikerbosrand NR include brown hyena (*Hyaena bruunnea*), black-backed jackal (*Canis mesomelas*), African rock python (*Python sebae*) and a number of bird of prey species, but these are present at low densities (Falls 1993). Therefore, the disadvantages of foraging in larger groups, such as increased competition for food (Shopland 1987, Sontag *et al.* 2004) and longer foraging time (Fritz and De Garine-Wichatitsky, 1996, Stacey 1986) outweigh the benefits. This would favour smaller troops in Suikerbosrand NR.

Predation pressure affects how animals forage (Cowlishaw 1997). Previous studies in chacma baboons have shown that in the absence of predation pressure, troop size decreased and the occurrence of sub-trooping behaviour increased, while competition for resources remained relatively low (Barton *et al.* 1996).This appeared to be the case in previous studies by Anderson (1982) on the baboon population in Suikerbosrand NR. However, with increasing population density there is likely to be an increase in resource competition and despite the occurrence of sub-trooping behaviour, inter-troop interactions are likely to increase (Barton *et al*. 1996).

4.5 Foraging patterns and space use

In recent years, the increasing baboon population size in Suikerbosrand NR has lead to concerns by management regarding the number of baboons the reserve can sustain without negatively affecting the overall biotic diversity. Movement patterns assess how animals exploit spatially distributed resources (South 1999). On a broad scale, movement patterns, such as changes in home range use give an indication of resource availability and habitat heterogeneity or uniformity (Nams 2005).

4.5.1 Home range size and population density

The home range size of troops was expected to differ in relation to troop size and habitat availability; home range size would expand and contract seasonally, reflecting seasonal variation in food availability. Previous studies in yellow baboons (Stacey 1986) and olive baboons (Barton *et al*. 1992) showed home range size to be proportional to troop size. Contrary to predictions, home range size remained constant seasonally and did not differ between troops. The absence of changes in home range size indicates that although season may be important as a factor associated with foraging, a troop's home range is relatively stable regardless of seasonal changes in the environment.

It is also possible that troop home range size is constrained by the space available within the reserve. A study of a North American marten species (*Martes americana*) indicated that the lack of seasonal variation in home range size was apparently due to limited space when population density was high, and the need to ensure access to resources in winter months (Phillips *et al.* 1998). Discussions with the management of Suikerbosrand NR suggest that space has become a limited resource for baboons. Indeed, results from several censuses show that over the past 30 years, the baboon population has increased from approximately 300 individuals in 1974 to over 700 at present, and presently there are 12 known troops (Table 4.1).

The causes of increased population size include the absence of predators, diverse selection of food and other essential resources, and availability of alternative food resources from adjacent farms, urban areas and tourist sites within the reserve (Cowlishaw and Dunbar 2000). Close proximity to human resources can benefit naturally occurring populations of animals. For example, subpopulations of endangered bighorn sheep (*Ovis canadensis*) in California (Rubina *et al.* 2002) and threatened helmeted guinea fowl (*Numida meleagris*) in KwaZulu-Natal, South Africa (Ratcliffe and Crowe 2001) experienced increased diet quality, reproductive rate and population density in fragmented habitats surrounded by urban and agricultural areas.

Additionally, Anderson (1981) found mean troop home range size was 24.5km^2, compared to 12.7km^2 in the present study. With increased population density in a smaller home range size, inter- and intra-troop competition (Van Schaik 1983) for resources (e.g. food, water, and sleeping sites) increases, so that space could become a defendable resource. However, the instances of territoriality in baboons are rare and only one study by Hamilton *et al.* (1976) investigated territoriality in detail. In the Suikerbosrand NR population, Anderson (1981) found troop interactions to be low, with only 10 interactions recorded over 12 months. When interactions occurred, they were non-antagonistic and troops avoided contact with one another (Anderson 1981). During the course of my study, only one instance of a possible troop interaction was observed: no fighting occurred but adult males were observed vocalizing, herding troop members and chasing other large males away from females.

Apart from decreasing intra-troop competition for resources (Anderson 1981), I suggest that sub-trooping may also reduce inter-troop competition. In this way, the movement patterns of smaller sub-troops within home range are more random, thereby decreasing the chance of interactions between neighbouring troops/sub-troops. However, it cannot be discounted the possibility that with increased population size inter- and intra-troop interactions have increased despite the occurrence of sub-trooping and potentially increased aggression due to an increase in competition for resources.

4.5.2 Habitat use and the influence of home range overlap

In Suikerbosrand NR, habitat use patterns in troops varied depending on the dominant vegetation types occurring within their home ranges. In troops characterised by savannah habitat (e.g. more than 50% woodland vegetation) and open habitat (e.g. more than 50% shrubland vegetation), home range use was a function of the availability of different vegetation types and seasonal availability of food resources. Contrary to predictions, habitat use in the dry season was concentrated in vegetation prevalent within home range, while in the early and late rain season habitat use expanded into other vegetation types within the home range. A similar pattern was found in a study on home range use in collared peccaries (*Tayassu tajacu,* Judas and Henry 1999), in which home range use was constrained in the dry season in response to food shortages and food patchiness, while in the early fruit season when food was abundant and widespread, habitat use was extensive within the home range.

In response to increased primary production of plant growth following controlled and accidental fires, habitat use increased in grassland vegetation in the early rain season in savannah and open troops. Similarly, Stirrat (2003) found that in the dry season, agile wallabies (*Macropus agilis*) used forest areas to forage for shrub leaves and fruiting plants, whereas in the wet season habitat use was opportunistic and wallabies foraged in open areas where high quality herbaceous plants were available. Conversely, in troops with mixed habitat availability, habitat use did not show any seasonal patterns and home range use was extensive.

I suggest that habitat use was influenced by habitat availability within home ranges (Anderson 1981), proximity to neighbouring troops (Cowlishaw 1997), and competition for resources between troops with overlapping home ranges (Barton *et al.* 1996). Below, I discuss how home range overlap and habitat availability affect habitat use of baboon troops in my study.

Home range overlap was high in optimal areas of the reserve with ideal food, water and shelter for baboons, as confirmed previously Anderson (1981). Consequently, there is a greater chance troops will share resources within overlapping areas. Therefore, it is possible that when resources are less abundant (e.g. in poorer habitats or in the dry season), that home ranges are less likely to overlap between troops. Evidence for this claim is provided by data from a concurrent study by Pahad (unpublished) of the same baboon population. Home range overlap was lower in the dry season than in the summer rainy months, indicating that when resources were abundant in the summer months following initial rainfall, competition for resources was lower, while in the dry season, when food availability was scarce, competition was greater, and therefore home range overlap decreased (Pahad unpublished).

Habitat availability could have also influenced habitat use in troops. Open and savannah troops showed seasonal habitat use in grasslands, whereas troops in mixed habitats showed consistently greater grassland use regardless of seasonal availability of food resources. Similarly, habitat use in Japanese macaques (*Macaca fuscata*)was influenced by both seasonal availability of primary food sources within its home range and competition for resources with neighbouring troops, so that macaques avoided areas of their own home range even when preferred food was available (Tsuji and Takatsuki 2004).

4.6 Foraging strategies and foraging model

Optimal Foraging Theory (OFT) emphasises the evolutionary importance of foraging behaviour and the consequences on the reproductive fitness (Stephens and Krebs 1986, Yearsley *et al.* 2002). This theory predicts that an animal will forage in a manner that minimises the demands and risks of foraging, while maximising overall energy intake (Schoener 1971). Perry and Pianka (1997) suggest OFT should be used as a framework from which to test hypotheses and make predictions, where foraging models predict optimal foraging strategies (i.e. maximising foraging success rather than overall energy intake), usually by the use of mathematical models.

A foraging strategy describes the ways in which animals maximise energy gain while minimising the cost of foraging under different environmental conditions (Mckenna 1982). Two foraging strategies have been associated with baboon foraging effort: energy maximization and energy conservation (Barton *et al.* 1992, Post 1984). When faced with low levels of resources, an animal can forage more, troops travel longer distances to find as much as possible, and expend more energy trying to find scattered or patchy resources (Jolly 1985). Alternatively, animals can conserve energy by lowering energy expenditure of travelling and instead concentrating foraging effort on resources that are widespread but of lower quality (Jolly 1985). From my findings, I formed a simple foraging model based on the potential energy gains/costs from foraging under different environmental conditions (Table 4.3).

Two foraging strategies were identified according to seasonal patterns of foraging and diet in baboons in Suikerbosrand NR. In the dry season, environmental conditions (e.g. cold temperatures or shorter day lengths) lead to foraging constraints, greater thermoregulatory cost and energy need. Rather than increasing foraging effort, baboons cope with increased energy demands by foraging conservatively (i.e. focussing home range use and expanding diet to include whatever is available (Table 4.3). This, I suggest, minimises energy expended on foraging activities. Conversely, in the early and late rain season, baboons maximise energy gain by increasing foraging effort - opportunistically using habitats within their home ranges and concentrating diet in response to seasonally abundant food types. Therefore, baboon foraging behaviour and diet are constrained by the seasonal availability of food resources, and foraging effort is directly proportional to resource availability (Figure 4.2). This is in contrast with previous studies on foraging effort in baboons, where foraging effort was inversely proportional to food availability (Barton *et al*. 1992). When the cost of foraging exceed the benefit, baboons minimise energy expenditure and forage conservatively; when the energy gain from foraging exceeds the cost baboons maximise energy intake by increasing foraging effort (Figure 4.2).

Table 4.3 Seasonal differences in environmental factors and subsequent foraging response by chacma baboons in Suikerbosrand Nature Reserve.

Comparison of seasons		
Season	Dry	Early and late rain
Environmental conditions	Low/absent rainfall	High rainfall
	cold minimum temperatures	warmer minimum temperatures
	shorter day lengths	longer day lengths
Food availability	Low	Abundant
Resource distribution	Scattered	Widespread
Foraging response		
Behaviour	manipulate more/search and consume less	search, manipulate* and consume more
Foraging effort	Decrease	increase
Habitat use	Intensive	opportunistic
Diet	Broad	narrow
Raiding	Yes	opportunistic

*Manipulate behaviour was low in the late rain season

Although I did not use a mathematical model to assess foraging in baboons in Suikerbosrand NR, my model allows me to evaluate foraging behaviour by baboons in relation to OFT. My findings show that baboons in Suikerbosrand NR use optimal foraging strategies to maximise energy gain and minimise foraging cost under seasonally variable environmental conditions.

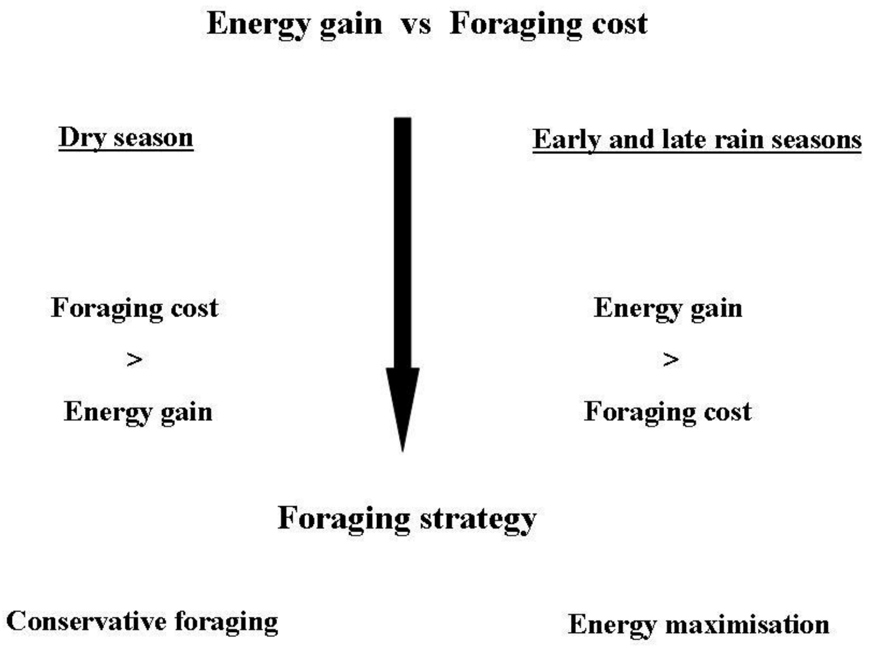

Figure 4.2 Overview of foraging model and seasonal foraging strategies in the baboon population in Suikerbosrand Nature Reserve.

4.7 To raid or not to raid?

A number of factors contribute to the occurrence of raiding behaviour in baboons especially when a protected area is adjacent to agricultural and urban environments (Hill 1997). In spite of access to easily available high-energy foods (Cowlishaw and Dunbar 2000), decreased availability of areas within the reserve to disperse can lead to raiding.

Overall, the diet of troops was similar, except for maize, which occurred in very low proportions in several troops and was particularly high in one troop. The occurrence of maize in the dung was greater in troops along the western and southern boundaries of the reserve, where although there were no significant seasonal patterns in maize consumption, maize was found more often in dung collected during the dry season compared to the early and late rain seasons. Anderson (1981) observed raiding behaviour previously in baboons in the Suikerbosrand NR, where one troop in particular, located on the southern border of the reserve, raided neighbouring maize farms more frequently in the winter months (April – August).

Maize is an ideal source of food for baboons because the plant and fruit (kernels) are high in carbohydrates, protein, fat and minerals (Du Plessis, 2003). In South Africa, maize can be harvested from the end of March until the middle of July (Hawkins pers. comm. Grain South Africa). It is still possible for baboons to access maize crops at other times as well, since they are known to eat unripe green fruit as well as ripe kernels, which have been left in fields. Farmers are known to leave maize in the field (i.e. not harvested) during winter when rainfall is low (Hawkins pers. comm., Grain South Africa), providing opportunities for raiding in winter.

It is possible that in my study maize was both under- and over estimated (due to the opportunistic nature of raiding and limited monthly sampling periods). However, evidence from dung analysis and a questionnaire survey (Pahad unpublished) indicate that raiding behaviour may have become an alternative mechanism of coping with increased population pressure, especially when resource availability within the reserve are constrained (i.e. the dry season). In support, Pahad (unpublished) found that three troops spent between 40% and 70% of their time outside the reserve boundaries; five troops spent between 2% and 5% outside the reserve; only two troops were found exclusively within the reserve.

4.8 Future studies and management suggestions

This study considered factors affecting foraging behaviour in a population of chacma baboons in a small grassland reserve. Clear seasonal patterns emerged which suggested that baboons used different strategies to cope with changing environmental stressors. Far less certain was the influence of spatial elements on foraging behaviour, movement patterns and troop dynamics. Results suggest that factors such as habitat assemblage, resource quality and availability influence troop size, foraging effort and home range requirements.

Foraging patterns indicated that the availability of specific habitat types and resources within home range influence habitat use. Unfortunately, habitat sampling was not performed in my study, and future studies comparing areas where baboons concentrate foraging effort and areas least used would give a better indication of the impact of baboon foraging on biotic diversity.

Continued sampling of baboon diet is needed in order to establish precisely what baboons consume. For example, seeds found in scat can be grown to identify plants. Baboons alone may not be responsible for changes in the biotic components within the reserve, and it is necessary to establish the effect other animal species (e.g. eland, kudu, rodents, and guinea fowl), and abiotic factors (e.g. fire) have on biodiversity. Additionally, a future study on diet could assess the energy gain derived from different food types seasonally (e.g. fruit, tubers, seeds, invertebrates and maize) in relation to the energy costs of foraging, which could give more detailed information regarding baboon foraging strategies.

Speculations that the population of chacma baboons has become too large cannot be confirmed or refuted. According to Cowlishaw and Dunbar (2000) the size, growth and carrying capacity of a population is controlled by factors such as food availability, predation pressure, population dynamics and genetic diversity where a population will reach carrying capacity when the food resources within a habitat can no longer sustain a population size.

The growing conflict between baboons and farmers in is a continual concern for management of nature reserves. Further research is needed to assess farms most at risk, times when farms are most likely to be raided and what crops are most likely to be damaged. Information is required about which troops or individuals are raiding and the areas outside the reserve that are being exploited (e.g. patches of natural vegetation, human refuse and/or croplands). My findings indicate that baboons within the reserve cope with reduced food availability and increased energy demands in the dry season by minimising foraging effort (i.e. by searching less, decreasing distance travelled and broadening diet), whereas in the rainy season, baboons increase foraging effort (i.e. searching and consuming more, increasing distance travelled and narrower diet). This creates the potential for baboons to come in contact with agricultural and urban areas in the rainy season. However, it cannot discount the fact that baboons are opportunistic foragers; therefore raiding behaviour is more likely to occur when resources are less abundant (i.e. dry season). This may be exacerbated by competition between troops for limiting resources. Continued monitoring of troops in the western and southern regions is recommended in order to assess which areas outside the reserve are targeted by the troops, and the frequency and intensity of the raiding activities.

4.9 Conclusions

My study has confirmed our knowledge of the behavioural adaptability of chacma baboons under challenging environmental conditions, and highlighted issues concerning the management and conservation of isolated populations surrounded by agricultural and urban areas. Chacma baboons in the Suikerbosrand Nature Reserve modify their behaviour in order to cope with seasonal changes in food availability. Clear seasonal patterns emerged suggesting that baboons use different foraging strategies to cope with changing environmental stressors. Raiding behaviour is not new in this population but is likely to continue under high population density and in seasons with high foraging cost and food limitations.

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Appendix: Plant species

List of common plant species found in Suikerbosrand Nature Reserve (Falls 1993).

Plant form	Species name
Grass	*Aristida transvaalensis*
	Cymbopogon excavatus
	Eragrostis plana
	Ehrharta erecta
	Panicum maximum
	Melenis repens
	Themeda trianda
	*Eustachys paspaloides**
	Trachypogon spicatus
	*Heteropogon contortus**
	Panicum natelense
	Diheteropogon amplectans
Tree and Bush	*Acacia caffra*
	Acacia karroo
	Englerophytum magalismontanum
	*Rhoicissus tridentata**
	*Kalanchoe rotundifolia**
	Protea caffra
	*Ledebovria ovatiflora**
	*Leonotis dysophylla**
	*Rhus sp.**
	*Cussinia paniculata subsp. Paniculata**
	*Ziziphus mucronata**
	*Viscum rotundifolium**
	Leucosidea sericea
	Celtis africana
	Kiggelaria africana
	Halleria lucida
	Buddleia salvifolia
	Cassinopsis illicifolia
	Euclea crispa, Euclea undulata**
	Diospyros lycoides

Shrub	*Cyrtanthus breviflorus**
	*Veronia natalensis**
	*Berkheya setifera**
	*Chrysanthenoides monilifera**
	*Gazania kresiana**
	Senecio sp.
	Helichrysum sp.
	*Kalanchoe thrysiflora**
	*Argyrolobium cf. velutinum**
	*Eriosema cordatum**
	*Hypoxis sp.**
	*Bulbine abyssinica**
	Stoebe vulgaris
	Indigofera sp.
	Nidorella sp.
	*Berkheya seminivea**
	*Agapanthus campanulatus**
	*Sphenostylis angustiflora**
	*Erythrina zeyheri**
	*Crinum bulbispernum**
	*Striga elegans**
Succulent	*Aloe greatheadii var. davyana*
	Aloe marlothii
	Aloe transvaalensis

* Species identified by author