# THE FEEDING ECOLOGY AND HABITAT USE OF LIONS REINTRODUCED TO SMALL, ENCLOSED RESERVES IN THE EASTERN CAPE PROVINCE, SOUTH AFRICA

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# ABSTRACT

Lions have recently been introduced to a number of small (<300km$^2$), enclosed reserves in the Eastern Cape Province as a draw-card for tourists. However, there have been few studies of lion behaviour or predator prey interactions within small reserves. Thus the aim of this study is to contribute towards a better understanding of the effects of space on diet and habitat use of re-introduced lions. The research was conducted at two small private reserves, Shamwari and Kwandwe. Kills were mostly large (55%, >120kg), adult (41%) and male (39%) and the five most commonly killed species (kudu, black wildebeest, warthog, bushbuck and Blesbuck) comprised 67.9% of all kills and 67.8% of total biomass consumed. In an attempt to overcome the problem of gaps in the kill lists, a subset of data, which excluded kills more than five days apart, was analyzed and this gave similar results to analysis of the full kill lists. Mean daily intake rates varied annually between 2.26 and 5.23kg.FEQ$^{-1}$ for the full data set and 4.53 and 10.46kg.FEQ$^{-1}$ for the subset. The difference between estimated (calculated using daily intake rates of 5 and 7.12kg.FEQ$^{-1}$) and observed offtake for each ungulate species reflected the preference ratings for that species. Analysis of bone marrow indicated that: lions killed ungulates in moderate to good condition; condition of culled animals was lower than that of kills; distal bones could be used in analyses; and that that bones exposed to the environment for at least a week could be used to analyze condition of prey. Home ranges and activity centers ranged from 21.42km$^2$ to 73.27km$^2$ and 2.71km$^2$ to 17.47km$^2$ respectively, which was smaller than expected from previous studies. Although, lions at Kwandwe and Shamwari preferred different vegetation types, at both reserves they generally occupied areas that were structurally similar to what has

previously been reported. Continuous monitoring and analyses of diet, including condition of the prey, and habitat use will provide reserve managers with some of the necessary information to enable them to effectively manage their lion populations and to predict and minimize potential problems.

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# PREFACE

The thesis is structured as follows:

**Chapter 1** introduces the broader conservation implications associated with reintroducing lions to small, fenced reserves and that are important to the management implications discussed in this project. The aims of this research are given in this chapter.

**Chapter 2** provides a general description of the two study sites, Shamwari and Kwandwe Private Game Reserves, with notes on vegetation types and the predators present on each site

**Chapters 3 and 4** look at various different aspects of the feeding ecology of reintroduced lions. In addition, Chapter 3 provides a method of improving data quality and discusses a method of estimating annual offtake and Chapter 4 evaluates the bone marrow analysis technique.

**Chapter 5** looks at the characteristics of home range, habitat selection and habitat use by lions in small, closed reserves.

**Chapter 6** is a general discussion of the results of the project and also discusses management implications of the findings.

Scientific names for all species mentioned in the test are given in Appendix A.

# CHAPTER 1

# Conservation implications of reintroductions of lions to small, fenced game reserves in South Africa

## INTRODUCTION

Lions, which were once common through Europe, over much of Asia and the African continent (Skinner & Smithers 1990), have undergone one of the most extensive range contractions of all mammalian predators over historical times (Schaller 1972; Skinner & Smithers 1990). They have now been extinct in Europe for almost a thousand years and there are only between 200 and 250 individuals of the Asian subspecies living in the Gir National Park and Sanctuary in India (Jhala *et al.* 1999). The Asiatic lion (*Panthera leo persica*) is listed on the IUCN Red Data List as Critically Endangered (Internet ref. 1) and is protected under CITES Appendix 1 (Internet ref. 2). Census data indicate that the population is growing at a very slow rate ($r = 0.022$; Jhala *et al.* 1999) and is therefore extremely vulnerable to extinction if an unfavourable event, such as an outbreak of disease or drought, were to occur. In Africa, lions have been extinct in the northern part of the continent since disappearing from Morocco in 1920 (Skinner & Smithers 1990) and their distributional range in the southern regions has been considerably reduced. Throughout most of their current range, lions are becoming increasing rare outside protected areas. The numbers of the African subspecies (*Panthera leo leo*) have declined from an estimated 100,000 to 200,000 twenty years ago to around 23,000 at the current time (Nowell & Jackson 1996; Bauer & van der Merwe 2002; Pain 2003). They are protected from trade under Appendix II of CITES (Internet ref. 2) and listed on the IUCN Red Data List as Vulnerable (Internet ref. 1).

In South Africa, renewed interest in the country as an ecotourism destination has brought about a shift in land use from agricultural practices, which are usually in conflict with conservation, to game farming by government, private landowners and rural communities. Large predators, such as lions, which were eradicated from their natural ranges in South Africa in the late 1800s and early 1900s as a result of conflict with humans (Anderson 1981; Skead 1987), are now being reintroduced in an attempt to increase tourism to the country. Reintroduction has been described as the intentional movement of an animal, by humans, into an area of its native range from which it has disappeared, with the aims of establishing a self-sustaining and viable population (Stanley Price 1991), maintaining genetic heterogeneity and restoring natural ecosystems and ecosystem functions or processes (Breitenmoser *et al.* 2001). However, reintroductions of large carnivores are not always successful (Anderson 1981; Reading & Clark 1996; Linnell *et al.* 1997; Breitenmoser *et al.* 2001) and they are often controversial and cause conflict between reserves and surrounding farmers and communities (Breitenmoser *et al.* 2001; Sillero-Zubiri & Laurenson 2001); they can lead to the local decline or even extinction of some ungulate populations (Hunter 1998); and many large carnivore introductions have been to small reserves which are closed systems and therefore require continual management.

## SUSTAINABLE REINTRODUCTION AND RESERVE SIZE

The sustainability of reintroductions depends, in part, on the size of the receiving reserve. The classification of reserves according to size is a complex issue. Ideally, a reserve should preserve ecosystem functions (Beier 1993) and as such its minimum size depends on the purpose for which the reserve was created. An area which is set aside to protect a highly localised species with a small home range and naturally high density does not have to be as large as one which aims to preserve a large carnivore, which may occur at low densities and which requires a large area in order to establish territories (see Woodroffe 2001). In addition, studies have shown that isolated populations are more likely to go extinct if they occupy small habitats than if they inhabit larger patches (see Woodroffe 2001). Woodroffe & Ginsberg (1998) considered the impact of habitat fragmentation on large carnivores throughout the world by comparing their persistence in reserves of various sizes that are found within the carnivores' historic ranges. This critical reserve size is independent of the home range size of the carnivores studied. Based on this work, they proposed that the critical reserve size, that is to say the area for which there is a 50% probability of population persistence, for lions is 291km$^2$. In other words, if a reserve was established with the intention of conserving lions, it should exceed this critical size. While this may represent a useful starting point, the space required to conserve lions will differ in different habitats and habitat specific minimum reserve sizes should be calculated. A reserve's suitability for carnivore reintroductions can also be evaluated in terms of standing herbivore biomass, and its carrying capacity for carnivores may be based on this value (see Coe *et al.* 1976; East 1984). The definition of a "small" reserve can also be based on genetic viability since the sustainability of a population is affected by inbreeding (discussed later). A "small" reserve would then be any system where sustainability depends on active management strategies such as breeding or feeding programmes. Clearly there are a number of factors in addition to space that are important in the determination of the critical reserve size for lions and they should all be considered when introducing lions.

In reality however, the majority of game ranches and reserves are established primarily as business ventures and very few exceed 200km$^2$. The smallest reserve in South Africa which claims to have a population of free-ranging lions is the Madjuma Lion Reserve, within the Mabula Game Reserve in the Limpopo Province, which has an area of only 15 km$^2$ (Power 2003). By contrast, the largest reserve in South Africa with free-ranging lions is the Kruger National Park which has an area of 20,000km$^2$. In addition, many of the more recently established reserves in South Africa consist of land that was previously used for grazing and agriculture and therefore include little, if any, pristine vegetation and this may reduce their effective size. For example, just over 10% of the Madjuma Lion Reserve is old agricultural land (Power 2003) which is now grassland and may not provide sufficient hunting cover for lions or quality grazing for herbivores. However, carrying capacities can vary over time and genetic viability is difficult to measure, making comparisons between reserves difficult. In line with this, small reserves referred to here are those that do not exceed 300km$^2$ since Woodroffe & Ginsberg (1998) show that in reserves that are smaller than this critical size there is a high probability of population extinction. .

## IMPLICATIONS OF LION REINTRODUCTIONS TO SMALL, CLOSED RESERVES

The consequences of lion reintroductions are three-fold; there are genetic implications associated with small, isolated lion populations; there are implications for other species on the reserve, including herbivores and smaller carnivores; and lastly there are the financial implications of maintaining a reserve as a functioning, but inevitably managed, ecosystem and as an ecotourism destination.

### *Genetic implications*

One of the fundamental problems in conservation biology is the risk of inbreeding within small, isolated populations (Soule 1987, Bjorklund 2003). Inbreeding influences important fitness determinants such as fecundity, survival, growth and susceptibility to environmental stress (Frankham *et al.* 2002; Bjorklund 2003). An example is the lion population in the Ngorongoro Crater in Tanzania, which is believed to have gone through a genetic bottleneck in the 1960s and all members of the population are descended from only 10-15 individuals (Fosbrooke 1963; Packer *et al.* 1991). High levels of inbreeding have been shown to increase sperm abnormality in lions and there is evidence that the reproductive performance of the lions in Ngorongoro has declined as a result of decreasing heterozygosity (see Packer *et al.* 1991). A second example is from the Umfolozi Game Reserve in South Africa. In larger ecosystems, the normal tenure of a pride male or a coalition of males lasts about two to three years (Bertram 1973) and under these circumstances, the chances of father-daughter matings are reduced. However, Anderson (1981) found that male tenure in Umfolozi Game Reserve exceeded three years and concluded that where sub-adult females have remained in their natal prides, inbreeding is likely to have occurred, although no noticeable effects were observed at that time.

Careful movement of animals between reserves, thus introducing new genotypes, can alleviate the problem of inbreeding in small reserves. In this way, the animals in a group of small reserves are managed as a metapopulation. Metapopulations are typically defined as populations that are discrete in space but connected to others by limited migration, each of which could not persist on its own but is viable as a whole (Pullin

2002). According to Frankham *et al.* (2002), "metapopulations typically have effective sizes that are less than the sum of their parts, due to extinctions and bottlenecks during recolonizations. They are likely to suffer more rapid inbreeding and fitness reduction than single large populations and the effects are likely to be worse with higher rates of extinction and recolonization". Therefore, the persistence of a metapopulation is dependant on the both the persistence of the subpopulations and the maintenance of genetic diversity within those subpopulations. In this regard, records should be kept, and exchange programmes designed so that the potential for loss of genetic diversity is overcome and not just delayed. It is important to ensure that, when reintroducing lions to a reserve for the first time or to maintain or improve the gene pool, the lions are not closely related to other lions that have already been introduced into the metapopulation, as this will ultimately undermine the effectiveness of an exchange programme. For example, it is common practice among reserves to sell off young offspring to neighbouring reserves rather than buying and transporting animals from further afield. Therefore, exchange programmes require a coordinating body, agreements between reserves and a willingness to participate by most, if not all, reserves that have reintroduced lions. Complications arise because reserves compete for the same tourist market and communications are often strained. In addition, some animals are more relaxed and easily viewed by guests, others are bigger and more impressive and therefore more popular with guests, and others are 'problem' animals which a reserve may simply want to get rid of. These are all considerations that need to be taken into account when transferring lions between reserves.

### *Effects on other species*

Interspecific competition and aggression among carnivores can restrict spatial distribution and habitat selection, reduce prey encounter rates and food intake, and increase mortality rates (Laurenson 1995; Durant 1998; Creel & Creel 2001). For some species, these effects limit the population density of the subordinate competitor (Laurenson 1995). For example, lions have been known to actively exclude other predators, such as wild dogs and cheetah, from their territories (Durant 1998). While this is a natural process and seldom has a significant effect on the competing species in open and/or larger systems, the effect within small reserves is amplified because the populations are smaller to begin with and their movements are more restricted. Interspecific competition with larger carnivores may be a factor limiting the viability of wild dog populations, for example Creel & Creel (1996) showed that there was a strong negative correlations between wild dogs and lions in an area of the Selous Game Reserve in Tanzania and they observed that wild dogs often moved away from the sound of lions roaring nearby. Competition between lions and wild dogs appears to be less intense than between wild dogs and hyaenas, but the tendency of lions to attack and kill their competitors is an important factor in the conservation of wild dogs, especially since between 27% and 50% of wild dog deaths of known cause are the result of direct predation on wild dogs by lions (see Creel & Creel 1996). Cheetah in the Serengeti are limited by poor recruitment, largely due to aggression by lions (over a period of 20 years, 79% of cheetah cubs were killed by lions), and cheetahs are sometimes found in higher densities outside protected areas than within them (Caro & Laurenson 1994; Laurenson *et al.* 1995). In Phinda Resource Reserve (170 km$^2$) in South Africa, Hunter (1998) found that although lions were only observed killing cheetah on three occasions in a little over three years, the potential for conflict and cheetah deaths was higher than observed. Hunter (1998) believes that the balance between areas of suitable habitat and pressure from competitors is a critical factor in the success of cheetah reintroductions, but this requires further investigation. In another small reserve (160 km$^2$), a pride of reintroduced lions has killed two cheetahs in a year (C. Bissett, Dept of Zoology, Rhodes University, unpub. data 2003). If a female cheetah with young cubs is killed, the cubs are unlikely to survive without human intervention. This is not only of conservation concern for the endangered cheetah, but also of financial concern for reserves that rely on the sale of important game species. Thus the reintroduction of lions to small reserves is complicated by the presence of other carnivores. According to Creel *et al.* (2001), the implication of the aggressive interactions between lions and smaller carnivores is that protected areas will require separate habitat types suitable for each species in order to preserve complete carnivore guilds. Research suggests that reserves that support high densities of lions will only be able to support low densities of wild dogs or cheetah (see Durant 1998; Vucetich & Creel 1999). Macdonald (2001) states that "carnivore conservation is not just about saving rare species, but also prudently managing abundant ones". While this statement was made about conservation on a large scale, it is also relevant to small-scale systems where some carnivores may be abundant and others rare. At a worldwide scale, the number of free-living lions is declining (Pain 2003) but at small-scale levels, such as private reserves, they often have to be managed as the predominant carnivore.

Apart from being strong competitors, lions are also effective predators. Some studies have shown that where movement and migration are restricted or altered, herbivores may be more vulnerable to predation (Smuts 1978; Berry 1981; Mills & Shenk 1992; Hunter 1998) and lions might have significant effects on herbivore populations. Following the reintroduction of lions to a reserve, the lion population will be expected to increase. As the predator population increases, the increased demand for food will result in a comparative increase in predation on selected species. Predator-prey theory predicts that when the effort required to seek out and kill an animal of a particular species becomes too high, a generalist predator will switch to a more abundant prey (Dunham 1992; see Honer *et al.* 2002). This phenomenon is often most obvious in areas where some prey species migrate while others are sedentary. During the months when the migratory species are available, lions will often select that species over other available species. However, when the migratory species leave the area, the more sedentary species are selected (Rudnai 1974; Mills & Shenk 1992; Viljoen 1993). Under normal circumstances, the numbers of the first species will increase. This theory holds true in large reserves where there will be areas in which the prey can escape, recover and then repopulate other areas. However, in a small reserve there are likely to be few refuges and as a result carnivores will be able to reduce the prey to a level from which they might not be able to recover, a situation known as the Allee effect (Allee 1932; Stephens & Sutherland 1999) Lion numbers will continue to increase until something brings about a reduction in population growth rate either through a reduction in litter size, increased cub mortality or perhaps increased adult mortality, or through active removal of individuals by reserve management. The effects of lion reintroductions on resident herbivore populations are discussed in more detail in Chapters 3 and 4.

*Financial implications*

Many game species are introduced to reserves for tourism purposes and their value is determined by the amount of income they generate from tourism and at game auctions. Buffalo are considered one of the 'Big Five' and as such draw more tourists than other species, and disease-free buffalo fetch a high price at game auctions. However, in some areas, especially where lion density is high, lions have been known to favour buffalo above all other species (Funston *et al.* 1998). Such predation may result in reduced sightings of buffalo by tourists and a financial loss to the reserve through the loss of animals that could have been sold at auction. In a small reserve (180 $km^2$) in the Eastern Cape Province, it was estimated that ten lions (six adults and four cubs) consumed approximately R500 000 worth of game of various species in a single year (J. Rapson, Dept of Zoology, Rhodes University, unpub. data, 2002). This value will vary depending on the number of lions and the composition of their diet, but illustrates the high cost of maintaining a lion population on a reserve of limited size. The aggressive behaviour of lions towards other predators will also cost reserves financially if managers choose to maintain populations of more than one large predator within their reserve.

## CURRENT RESEARCH

Although lions are one of the most extensively studied carnivores in Africa, most of this work has been conducted in large, open systems such as the Serengeti and Ngorongoro, and very little research has been conducted on small reserves. There is a growing number of small, fenced reserves in South Africa where research is taking place, and some examples are given in Table 1. The information gained from these projects will better enable researchers to estimate carrying capacity for lions on small reserves and will provide an information base which can be used for the effective management of lion populations and provide a better understanding of the species as a whole.

The effect that restricted space may have on carnivore behaviour and predator-prey dynamics is important when considering reintroductions of the species, particularly since many reintroductions are to small reserves. When one considers the area and population size required to maintain a viable, self-sustaining population of lions it becomes obvious that populations within small reserves will require continuous management and manipulation in order to remain viable. These management practices should be based on the knowledge gained from research in small reserves but very little has been done in this regard.

Table 1.1. Some small reserves in South Africa where lion research is taking place or has been conducted.

| **Site** | **Size ($km^2$)** | **Founder population** | **Research coordinator** |
|---|---|---|---|
| Shamwari[α] | 180 | 6 | Rhodes University |
| Kwandwe[α] | 160 | 4 | Rhodes University |
| Phinda[#] | 170 | 13 | University of Natal |
| Pilanesberg*[#] | 550 | 19 | University of Natal |
| Makalali[#] | 150 | 12 | University of Natal |
| Madikwe*[#] | 650 | 12 | University of Natal |
| Welgevonden[#] | 250 | 5 | University of Natal |
| Entabeni[#] | 25 | 4 | University of Natal |
| Madjuma[β] | 15 | 8 | University of Pretoria |

* Included here, although greater than $300km^2$, because they form part of the Small Populations Conservation Project initiated in 1996 as a collaborative project between the University of Natal (Durban, South Africa), the University of Minnesota (St. Paul, USA), the North West Parks and Tourism Board, KwaZulu-Natal Wildlife, and a number of private land-owners.

[#] http://www.lionresearch.org/current/safrica/hunter.htm

[α] This study

[β] Power (2003)

## CONCLUSIONS AND PROJECT AIMS

Large carnivores, such as lions, are often regarded as "flagship species" which draw more attention and funding (both directly through donations for the preservation of the species and indirectly through ecotourism) than other species. Consequently lions are being reintroduced to small ecotourism reserves throughout South Africa and the future of lions in South Africa cannot be separated from the tourism industry. Without tourism, lions would not be as actively conserved because of the financial costs and the intensive management that is required. Many lion reintroductions are to reserves that are too small to maintain a viable, self-sustaining population, and the carnivores and ungulates need to be intensively managed. The complexity of the system is compounded when reserves introduce several species of large carnivore that may compete for space as well as food. Clearly management decisions should be based on sound knowledge and it is hoped that the research currently underway at some small reserves in South Africa will provide the necessary data.

In this project and thesis I have used information and material collected from two small reserves in the Eastern Cape Province to address three separate, but interlinked questions in the management of large carnivores:

1. Diet - with the aim of developing a method of assessing the diet of lions based on the type of data that reserves are likely to collect, and to evaluate a method of predicting annual offtake by lions;
2. Condition of prey - to determine the impact that lions may have on prey populations by assessing the condition of animals killed by lions, and to evaluate the methods available for determining this; and
3. Selection and use of home ranges - to assess the lions' use of the space and habitat types available to them, and to compare this to lions in less restrictive circumstances.

Although these three questions address separate aspects of lion behavioural ecology, an understanding of diet and the ability to estimate offtake from the reserve, an appreciation of whether the lions are killing fit or unfit animals, and a knowledge of habitat selection and space use should all contribute to better, and more holistic, management of lions on small reserves.

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# CHAPTER 2

# The study areas

## INTRODUCTION

Two sites within the Eastern Cape Province of South Africa were selected for this study based on their size. Both reserves were less than 300km$^2$ and of comparable size. Lions were reintroduced to these reserves primarily for ecotourism purposes and in the interest of restoring natural ecosystem processes. The reserves are similar in size but differ in terms of vegetation and climate. This chapter gives an overview of each reserve including brief descriptions of the vegetation types and the lions on the reserve.

## SHAMWARI PRIVATE GAME RESERVE

Shamwari Game Reserve is located within the Alexandria and Albany districts of the Eastern Cape Province, approximately 65km from Port Elizabeth and 56km from Grahamstown (33°20'S, 26°01'E). The reserve covers an area of 180km$^2$ and is surrounded by privately owned farmland and other conservation concerns. Shamwari was established as a reserve in 1990, prior to which, the land was used for stock farming.

The reserve's major water source is the semi-perennial Bushman's River, which flows through the reserve for 27.6km. Several perennial dams and boreholes that were originally created for stock farming and irrigation purposes, are utilized by game as alternative water sources. Shamwari ranges in altitude from 196m in the south to 628m in the northern regions, with a corresponding change in topography from gently undulating hills to deep valleys and gorges.

Shamwari is situated in the spring-dominant rainfall region of the Eastern Cape Province and receives approximately 550mm of rainfall per annum (Low & Rebelo 1996;

Stone *et al.* 1998). However, bimodal rainfall is experienced during the autumn and spring months (O'Brien 2000). Frost can occur on cold winter nights, especially in the low-lying areas.

*Vegetation*

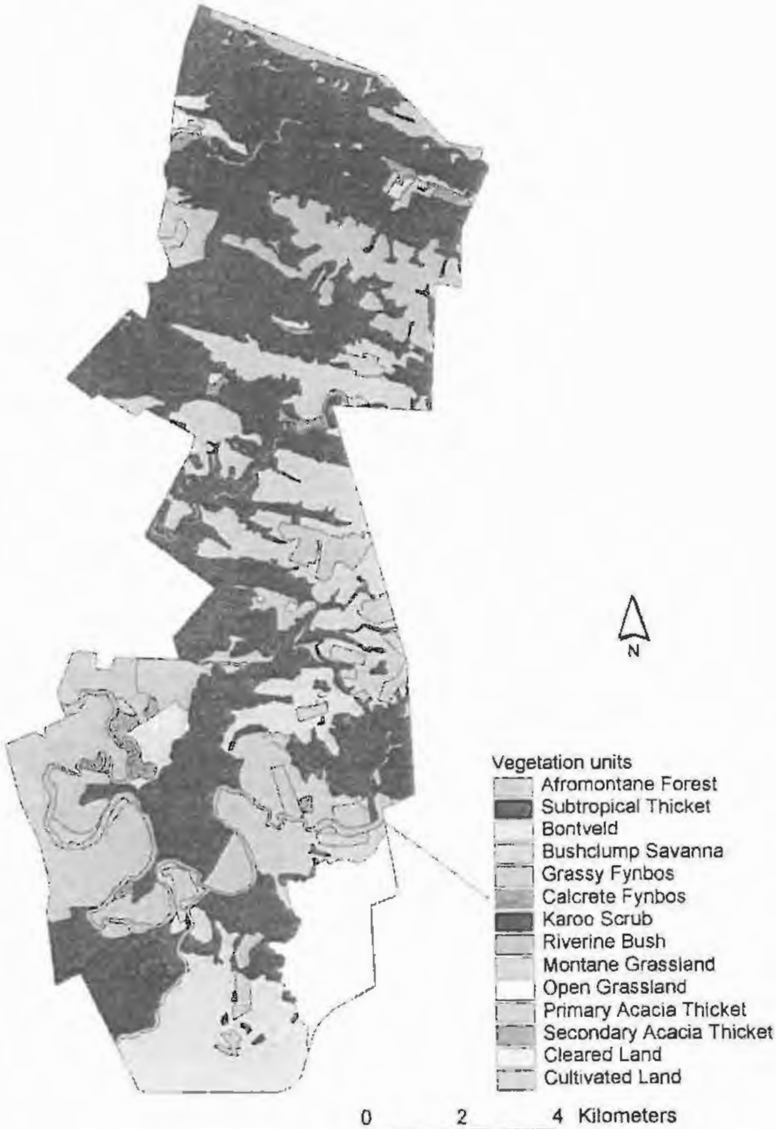

Figure 2.1. Map of Shamwari Private Game Reserve showing the different vegetation types and their distribution in the reserve.

The reserve is classified into fourteen vegetation types according to the classification system of Low & Rebelo (1996; Figure 2.1). The vegetation is dominated by Sub-tropical Thicket and areas of disturbed land where farming has altered the vegetation structure.

Afromontane Forest has a patchy distribution on the reserve, restricted to deep valleys with steep gradients where moisture is highest. It is characterised by numerous tall (30-40m) trees. Species such as *Podocarpus* spp., *Apodytes dimidiata*, *Halleria lucida* and *Calodendrum capense* are prevalent, while *Gymnosporia buxifolia*, *Scutia myrtina* and *Rhoicissus tridentata* dominate the shrub layer (Low & Rebelo 1996).

Subtropical Thicket is a very dense thicket of evergreen woody shrubs and trees found on the slopes of most of the hills in the reserve. *Cassine aethiopica*, *Euphorbia triangularis*, *E. tetragona* and *Plumbago auriculata* are indicator species of this vegetation type (Low & Rebelo 1996). Subtropical Thicket accounts for 44.2% of the total area of the reserve.

Bontveld is restricted to the flat and moderately sloped calcrete soils in the south of the reserve. The vegetation consists of bushclumps interspersed with grass and/or Karroid shrubs. The bushclumps in the Bontveld are typically composed of several *Rhus* spp., *Canthium inerme*, *Zanthoxylem capense*, *Scutia myrtina* and *Grewia occidentalis* (O'Brien 2000). .

Bushclump Savanna has the same basic structure as Bontveld in that it consists of bushclumps of several *Rhus* spp., *Pappea capensis*, *Schotia afra* and *Carissa haematocarpa* interspersed with Karroid shrubs such as *Pentzia incana* and several grass species. It only occurs on deep soils, without calcrete substrata in the southern part of the reserve (O'Brien 2000).

Grassy Fynbos is only found on the quartzite ridges in the northern part of the reserve. These communities are a complex mixture of grasses, woody shrubs and small-leaved Fynbos elements. Characteristic species of this vegetation type are *Leucadendron salignum*, *Passerina vulgaris*, *Aspalathus chortophila* and *Metalasia muricata* (O'Brien 2000).

Calcrete Fynbos is limited to a very small area of 0.008km$^2$. In terms of size this is insignificant, but due to the vulnerability of the indicator species, *Syncarpha recurvata*, it warrants special conservation status and is thus included as a vegetation unit.

Karoo Shrubland is analogous to Eastern Mixed Nama Karoo described by Low & Rebelo (1996) and is only found in the southwestern part of the reserve. It is a mixture of grasses and shrubs and dependent on seasonal rainfall (Low & Rebelo 1996). *Pentzia incana* and *Eriocephalus ericoides* are indicator shrub species while *Pappea capensis* and *Acacia karroo* comprise the small tree component.

Riverine Bush (Riverine Thicket) is limited to the banks of the Bushmans River and some temporary watercourses. It has a moderate to very dense vegetation structure. *Combretum caffrum, Acacia caffra* and *Plumbago auriculata* are characteristic of the vegetation type (O'Brien 2000).

Montane Grassland occurs only on quartzite ridges above Subtropical Thicket at an altitude greater than 400m. These areas are dominated by *Themeda triandra, Eragrostis curvula* and *Sporobolus fimbriatus* but can be invaded by thicket species in the absence of bulk grazers (O'Brien 2000).

Open Grasslands are only found in the south of the reserve. *Themeda triandra, Eragrostis curvula* and *Digitaria eriantha* dominate the vegetation of the area (O'Brien 2000).

Primary Acacia Thicket is generally found on the low-lying flat land of the reserve, near water courses. It is often found in areas that were previously cleared for agriculture. It is dominated by *Rhus longispina* with some *Acacia karroo*. Other characteristic species include *Azima tetracantha* and *Gymnosporia polycantha* (O'Brien 2000).

Secondary Acacia Thicket occurs where Primary Acacia thicket has been disturbed either through overgrazing or mismanagement. *Acacia karroo* dominates these thickets with very few *Rhus longispina* and *Azima tetracantha*. When combined the Primary and Secondary Acacia Thickets account for 7.4% of the total area of the reserve.

The Cleared and Cultivated Lands are disturbed habitats that have either been cleared to create crop lands or grazing for stock, or have been created by overgrazing by goats (O'Brien 2000). This vegetation type is typical of the area surrounding homesteads, on cut-lines and near the Bushmans River. *Azima tetracantha* and various grass species are often prevalent in these areas (O'Brien 2000).

*Predators*

Four adult female and two adult male lions were reintroduced to the reserve in October 2000. The six lions were initially separated into prides of two females and a male and released separately in the northern and southern parts of the reserve and are known as the Northern and Southern Prides respectively. The Northern Pride consisted of two unrelated females from Madikwe Game Reserve, South Africa that were originally bonded in a boma with a male from Pilanesberg Game Reserve, South Africa. The Southern Pride consisted of two sisters from Pilanesberg that were originally bonded with a male from Madikwe. The northern section is separated from the southern section by the Bushman's River, which the lions are able to cross. Both the Northern and Southern Pride females established home ranges in the areas in which they were released. The males, especially the Northern Male (NM), did not stay with the females they were bonded with and now move between the two prides. They have reproduced successfully and produced eleven surviving cubs between them. In November 2003, a subadult male and a subadult female were moved to another reserve. At present there are fifteen lions of varying ages on the reserve. Other large predators now present on the reserve include seven cheetahs, fourteen brown hyenas, four leopards and twelve wild dogs. The prey biomass on the reserve is approximately 2300kg.km$^{-2}$.

## KWANDWE PRIVATE GAME RESERVE

Kwandwe is a relatively new development that was opened to the public late in 2001. The reserve is located approximately 27km north of Grahamstown in the Eastern Cape Province (33°09'S, 26°37'E). It covers an area of approximately 160km$^{2}$, surrounded by mostly farmland and other conservation concerns such as the Great Fish River Reserve Complex, which lies on its eastern border.

The Great Fish River flows through the reserve for 42km and is perennial due to the Orange River water scheme. Several man-made dams and boreholes are present on the reserve and provide alternative water sources. Kwandwe ranges in altitude from 283m in the Great Fish River valley to 580m in the north-east. The reserve is dominated by steep valleys and gorges in the south and north-east and undulating hills in the central portion.

Rainfall is bimodal (spring and autumn) and varies between 400-550mm per year (Low & Rebelo, 1996). The reserve experiences hot summers, with daytime temperatures often exceeding 35°C, and cold winters, with daily maximum temperatures as low as 5°C and widespread frost (Stone *et al.*, 1998).

### *Vegetation*

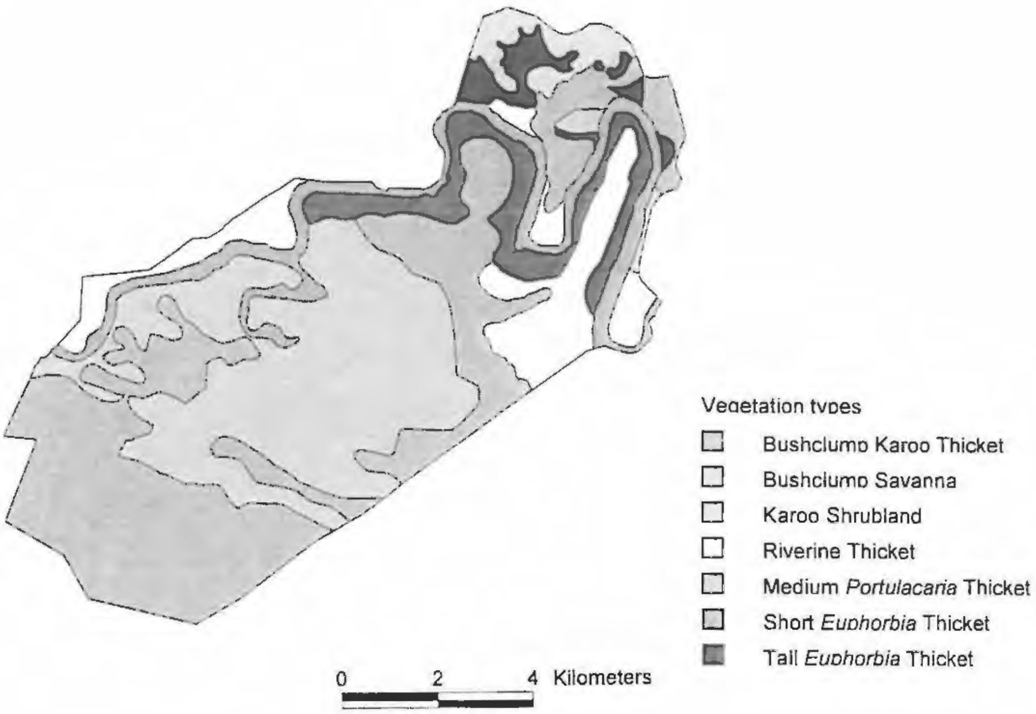

Figure 2.2. Map of Kwandwe Private Game Reserve showing the different vegetation types and their distribution in the reserve.

The vegetation on the reserve (Figure 2.2) is dominated by thickets, with Medium *Portulacaria* and Bushclump Karoo Thicket being the most abundant, and Karoo Shrubland being less abundant. Other vegetation types include Tall and Short *Euphorbia* Thicket, Riverine Thicket and Bushclump Savanna.

The Medium *Portulacaria* Thicket is analogous to the Xeric Succulent Thicket described by Low & Rebelo (1996). Xeric Succulent Thicket is dominated by a high proportion of succulent shrubs, trees and lianas as well as some sclerophyllous trees and shrubs (Low & Rebelo 1996). This vegetation is invasive in savanna and grassland vegetation in the absence of browsers such as black rhino and kudu. Indicator species include *Grewia robusta, Brachylaena ilicifolia, Portulacaria afra, Maytenus capitata* and *Rhigozum obovatum* (Low & Rebelo 1996).

Bushclump Karoo Thicket is characterised by *Euclea undulata, Aloe ferox* and *Schotia afra.*

Tall Euphorbia thicket is generally found on the slopes of the hills in the northern part of the reserve and is characterised by the presence of *Euphorbia tetragona, E. triangularis, Cassine aethiopica, Schotia afra, Pappea capensis* and *Euclea undulata* (Low & Rebelo 1996).

Short Euphorbia Thicket derives its name from the short (< 1m), succulent, *Euphorbia bothae* which dominates the vegetation type. Other important species.include *Euclea undulata, Rhus* spp., *Lycium* spp., *and Rhigozum obovatum.*

Riverine Thicket, as the name suggests, dominates the watercourses and most of the drainage lines within the reserve. Dense stands of *Acacia karroo* make up the bulk of the vegetation interspersed with some *Lycium* spp. and *Azima tetracantha. Pappea capensis, and Rhus longispina*

The Bushclump Savanna is analogous to the Bushclump Savanna found at Shamwari. However, *Pappea capensis* trees are more abundant.

*Predators*

Two adult female (F1 and F2) and two adult male lions (M1 and M2) were reintroduced to Kwandwe in October 2001. None of the lions were related, although M1 and F2 were both from Madikwe Game Reserve, South Africa and M2 and F1 were both from Pilanesberg Game Reserve, South Africa. The females have formed a pride and M1 is the pride male at present. M2 is solitary and does not often come into contact with the other lions. The females have both reproduced successfully and there are now the original adults, five sub-adult cubs (four male and one female) and a new litter of unknown number in the reserve, all of which were sired by M1. In November 2003, two subadults were moved to a nearby reserve. The major predators on the reserve also include eight cheetahs, six brown hyenas and an unknown number of leopards. The prey biomass on the reserve is approximately 4800kg.km$^{-2}$.

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# CHAPTER 3

# Feeding ecology and estimates of annual offtake

## INTRODUCTION

The feeding biology of lions, including diet and feeding behaviour, has been a major focus of research (Pienaar 1969; Schaller 1972; Eloff 1973; Rudnai 1974; van Orsdol 1982, 1984; Smuts 1982; Green *et al.* 1984; Mills 1984; Packer & Ruttan 1988; Packer *et al.* 1990, 1995; Stander 1990, 1992a; Ruggiero 1991; Scheel 1993; Viljoen 1993; Funston *et al.* 1998; Hunter 1998; Ogutu & Dublin 2002; Power 2003). This information is important in understanding many aspects of lion behaviour and ecology (Mills 1996) and can contribute enormously to an understanding of the potential affect that lions may have on their prey populations.

### *Lion diet*

Previous studies of the feeding biology of lions in Africa have shown that their preferred prey are medium (60-120kg; Bourliere 1963; Ewer 1973; Saba 1979; Ruggiero 1991) and large-sized ungulates (>120kg; Funston *et al.* 1998, 2001), often above the lion's own body weight (mean mass for females and males is 126kg and 190kg respectively; Skinner & Smithers 1990), although the modal prey size may differ between different regions (van Orsdol 1982; Sunquist & Sunquist 1989). The size of lion hunting groups may influence the efficiency of prey location, prey capture and the probability of hunting larger prey (Schaller 1972; Caraco & Wolf 1975; Packer & Ruttan 1988; Stander 1992a,b; Funston *et al.* 2001). For instance, Stander (1992b) found that although a single lioness can capture, subdue and kill prey up to the size of an adult zebra (260kg; van Rooyen *et al.* 1996), cooperation was essential in order to capture large and/or fleet-footed prey, such as springbuck, zebra and wildebeest, on the open, flat terrain of Etosha National Park, Namibia. Considerably larger species such as giraffe (average weight of

830kg; van Rooyen *et al.*1996), buffalo (750kg; van Rooyen *et al.*1996) and eland (300kg; van Rooyen *et al.*1996) are also taken, but usually by groups of more than three lions (Kruuk & Turner 1967; Pienaar 1969; Schaller 1972; Bertram 1979; Smuts 1979; Stander 1992b; Viljoen 1997; Funston *et al.* 2001). Lions also feed on a wide variety of smaller animals such as rodents (Eloff 1973; Stander 1992a), lagomorphs (McBride 1982; Stander 1992a), birds (McBride 1982; Ruggiero 1991; Stander 1992a) and reptiles. Lions have even been observed feeding on flying termites and locusts when large swarms appear (Pienaar 1969). Although not important as a food source, other carnivores are sometimes attacked and consumed (Kruuk & Turner 1967; Pienaar 1969; Viljoen 1997, Hunter 1998). Lions will consume carrion and will stay with a kill until it is finished, even if it is far from fresh (Ewer 1973; Skinner & Smithers 1990).

### *Prey intake rates*

In the Serengeti, many of the herbivore species migrate which results in wide fluctuations in local abundance of certain of the lions' prey species (Scheel & Packer 1995). Packer *et al.* (1990) found that females may increase their food intake during periods of prey abundance (also see Stander 1991) but van Orsdol (1982) found that food intake by lions in Uganda was related to hunting success and not prey abundance. Estimates of daily intake rates vary considerably both spatially and temporally (Stander 1992a; Viljoen 1997). When calculating daily intake rates for a population, the age and sex structure can be taken into account by recording intake rates in terms of Female Equivalent Units (FEQ; see Bertram 1979; Viljoen 1997; Hunter 1998; Packer 1990). The intake rates of males and cubs are thus a proportion of the intake rates of adult females. For example, since adult males eat 1.5 times as much as an adult female, they are the equivalent of 1.5 females or FEQs and if the daily intake rate is calculated as 5kg/FEQ/day then adult males eat 7.5kg per day. The minimum, maximum and mean daily intake rates which have been recorded per Female Equivalent unit (FEQ) are 4.3 kg/FEQ/day (Power 2003), 14kg/FEQ/day (Stander 1991) and 7.12kg/FEQ/day (see Appendix B) respectively. This variation is partly due to different predator to prey ratios, but is also due to the methods used to estimate intake. Some studies have estimated intake as the kill frequency, in other words the number of kills made per lion per year (see Saba 1979; Viljoen 1997) or per day (Viljoen 1997) with estimates ranging from 10 to 36.5 kills per lion per year (see Saba 1979). However, on their own, kill frequencies are of limited value due to the large variation in modal body mass of prey animals in different regions and therefore, while these data are useful in illustrating broad trends, comparisons between areas are difficult. According to Viljoen (1997), the estimated amount of food consumed allows a better basis for comparison between different areas. A more accurate method is to determine the edible percentage of carcasses and then to monitor the proportion of each carcass consumed and the number, age and sex of lions feeding off that carcass (Viljoen 1993; Funston *et al.* 1998; Power 2003). However, problems arise with the estimation of the percentage edible biomass as different researchers have used different estimates (see Mills 1992; Stander 1992; Viljoen 1993). Green *et al.* (1984) derived mean rates of food consumption of 5.97 ± 1.53 kg per lion per day using sodium influx rates. This estimate is based on a different physiological process and may reflect daily requirements more accurately than estimates derived from observations. However, a lion is capable of consuming more than the minimum mass of food required to maintain optimal physical condition.

### *Effects of lions on prey populations*

Erlinge *et al.* (1984) addressed the question of prey regulation by predators and presented evidence which suggest that vertebrate predators can regulate prey populations and promote between year population stability provided that alternative prey were available in excess and that the predator populations were intrinsically regulated. However in small reserves this system cannot be maintained since herbivore populations are generally small and predator numbers are intensively managed. In addition, the impact of predators on populations of prey species is not a straightforward issue but rather a complex aspect of predator ecology (Schaller 1972; Smuts 1978; Mills & Shenk 1992). For example, Berry (1981) identified a combination of predation by lions and disease as the major cause of the decline in wildebeest and zebra numbers in Etosha National Park during the 1970s. Similarly, in the Kruger National Park, predation by lions is believed to have played a major role in the initial decline in roan antelope numbers between 1986 and 1993 (Harrington *et al.* 1999) as well as wildebeest and zebra numbers during the 1970s (Smuts 1978; Mills & Shenk 1992). Smuts (1978) ascribed this, in part, to the abundance of natural and artificial water supplies which resulted in a change from natural mass migrations to a more fragmented and sedentary distribution pattern. These smaller groups of herbivores are more vulnerable to predators especially during the calving season (Smuts 1978; Mills & Shenk 1992). A similar pattern was found in Etosha National Park where gemsbok were preferentially selected by lions (Berry 1981). Here, gemsbok, a species which does not have high water requirements, were found concentrated around artificial water holes during the dry season. Under natural conditions, lions would not be able to survive in these areas during the dry season and the gemsbok would be free from predation for eight months of the year (Berry 1981). In contrast to this, Schaller (1972) found that in the Serengeti, wildebeest were dying from malnutrition and disease and that predation had little impact on the population decline. The difference between Kruger National Park and the Serengeti may be due to the ratio of lions to prey which is low in the Serengeti (1:2000) but much higher in the Central District of the Kruger National Park (1:110). It has also been suggested that changes in climate affect the relative susceptibility of different ungulate species to predation (Mills *et* al. 1995; Ogutu & Owen-Smith 2003) and that the population declines of sable, roan and tsessebe in Kruger National Park are primarily due to range contraction brought about by increased aridity and consequent habitat changes within the park (Ogutu & Owen-Smith 2003). According to Macdonald *et al.* (1999), predation alone may not be the cause of a population destabilization but that the effects of predation may interact with other sources of mortality to cause a collapse of the prey population. The complexity and variation in predation and the impact it has on herbivore populations highlights the need to analyse different areas and situations individually, and to compare areas with similar features.

### *Lion preference for prey species*

Some researchers have found that despite a wide choice of prey species and irrespective of the abundance of the prey species, lions will hunt according to preference (Pienaar 1969; Ewer 1973). However, there are also data that suggest that this is not always the case (Schaller 1972; van Orsdol 1982; Mills & Shenk 1992; Funston *et al.* 1998). During the early 1980s, buffalo were the most important prey item of lions in the riverine woodlands of Mana Pools National Park in Zimbabwe (Dunham 1992). After the droughts of 1983 and 1984, the number of buffalo using the riverine woodlands declined substantially. Dunham (1992) found that, in response to this decline the number of buffalo killed also declined and lions killed increased numbers of other large herbivores. In the same area in the 1960s, waterbuck were more numerous than buffalo during the dry seasons and, during these times, waterbuck became the principal prey (Jarman 1972). According to Sunquist & Sunquist (1989), the most profitable prey type for large felids would be the largest available prey that could be safely killed. However, the effects of search time, encounter rates, and the energetic requirements of capture also need to be considered. If large prey is scarce, search time may be increased to the point where it becomes energetically too costly for lions to hunt them. Smaller, more abundant prey might then be more profitable. Eloff (1973) found that in the Kalahari Desert, small mammals and juveniles (particularly gemsbok calves) constituted more than 50% of the lions' diet. In a similar situation in Etosha National Park, Stander (1992a) found that animals weighing less than 50kg constituted 73% of observed kills and 50% of estimated biomass consumed. Whether lions hunt according to abundance or preference may have important implications in the management of prey species, particularly if they select a species that is already rare or vulnerable. This appears to be the case in the Kruger National Park with the roan antelope, sable and tsessebe populations (Harrington *et al.* 1999; Ogutu & Owen-Smith 2003).

According to Mills & Shenk (1992) the data needed to measure the effect of predators on their prey include: the numbers of predators and prey in the area, how the predators select their prey with respect to species, sex, age and condition, how often predators kill, the fecundity and survival rates of the prey and the contribution of mortality other than predation to the population dynamics of the prey.

In this chapter, the diet of lions in Shamwari and Kwandwe is examined and compared in terms of species, sex and age of kills, the interval between kills and the average daily intake rate. Using a formula proposed by Goodman (unpubl. report & pers comm., Natal Parks Board, 2003), the expected annual offtake per species is calculated and compared to the observed offtake. A secondary aim of this chapter is to develop a method of analysis that extracts the maximum information from the type of data that is typically collected by a reserve.

## METHODS

### Data collection

Kills made by the lions since their reintroduction have been recorded by the reserve management on both reserves. These kill lists were based on opportunistic observations of lions at carcasses, and kills were mostly encountered when the reserve rangers were searching for the lions for tourist viewing. Opportunistic observations such as these are often biased towards large animals (Bertram 1979; Mills 1996) and small kills are often missed by this method. Kill lists based on opportunistic observation are therefore incomplete and the way in which this has been dealt with is discussed later. Reserves were visited at the start of the project and discussions held with managers as to the type of data that should be collected. In spite of this, too few data were collected for the Kwandwe lions, and it has only been possible to analyse the Shamwari data.

Kills by lions at Shamwari were recorded for a total of 36 months beginning in October 2000 when the lions were first released onto the reserve. In this study the 36 months have been divided as follows: Year 1 – October 2000 to September 2001, Year 2 – October 2001 to September 2002, and Year 3 – October 2002 to September 2003 to give three full years.

For all kills the species, lions(s) present and the date were recorded and wherever possible, sex, age and location and/or GPS readings of the carcass were recorded. Age categories were defined as:

| | |
|---|---|
| juvenile | small, dependant calf; |
| subadult | young, independent animal not fully grown and not reproductively active; and |
| adult | full grown, reproductive animal. |

### Data analyses

Kills were analysed in terms of species, age, sex and size in order to determine the preferences of the lions. There is considerable variation in the assignment of species to size classes in the literature, therefore species were assigned to a size class according to the categories used by Hunter (1998; Table 3.1) both in the analysis and when comparing this study to previous studies. Kills were not analysed seasonally due to the inconsistent search effort during the year which was largely due to the fluctuating volumes of tourists with a peak in the summer months.

Table 3.1. Size categories of prey (as used by Hunter (1998)) and examples of each.

| Kill Size | Weight range | Typical examples |
|---|---|---|
| Small | <60kgs | Bushbuck, common duiker, impala, mountain reedbuck, springbuck |
| Medium | 60-120kgs | Blesbuck, ostrich, red hartebeest, warthog |
| Large | >120kgs | Eland, gemsbok, giraffe, kudu, wildebeest, waterbuck, zebra |

### *Prey Preference*

To determine whether lions selected certain species preferentially, a preference index was calculated (Pienaar 1969) for prey species. Calculations were not made for species such as black springbuck and blue wildebeest, which were removed from the reserve during the course of the study, and those species for which adequate game count records were not available. The preference ratings were determined as follows:

$$\text{Preference} = \frac{\text{relative frequency of prey in diet}}{\text{relative abundance of prey}}$$

The relative frequency of prey in the diet was calculated as the number of individuals of a particular species, killed by all lions, as a proportion of the total number of individuals of all species killed over a particular time period. The relative abundance of prey was based on game counts derived from an aerial census method and was the number of a particular species as a proportion of the total number of all species preyed upon by lions. This method tends to underestimate the relative abundance of species such as warthog, which run for burrows when chased, and small, forest dwelling ungulates such as duiker and bushbuck. A preference index of one, or close to one, indicates that the species was selected according to its abundance on the reserve. An index above one shows that the lions are preferentially selecting for the species and an index of below one indicates that the prey species is not actively hunted and is avoided when it is encountered opportunistically.

### *Interval between kills (kill rate)*

The average interval between kills was calculated in order to determine the average daily intake rates of lions. To do this, the lions, were divided into the two prides, Northern and Southern (see Chapter 2), for analysis. The presence or absence of the pride males was not taken into account as this was highly variable. It was assumed that the females would catch the same prey regardless of the presence of a male as males do not often assist in hunting (Schaller 1972; Mills & Shenk 1992; Stander 1992a,b). Too few data were collected for the males to analyse their kill rates individually although male lions can and do hunt independently of females (Funston *et al.* 1998). Using the recorded kills, the period (in days) between consecutive kills by the same pride was calculated.

### *Calculation of daily food intake*

The biomass consumed by lions was calculated from the kill list using the mean mass of the prey species taken from van Rooyen *et al.* (1996). The edible percentage of carcasses was estimated from the categories suggested by Viljoen (1997) of <50kg: 80%, 50-150kg: 75%, 151-250kg: 70%, 251-500kg: 65%. These calculations were done at species level and age and sex of individuals were not taken into account in the calculation due to the incompleteness of the data.

Adult male lions eat 1.5 times as much as females (Schaller 1972; Funston *et al.* 1998), subadults aged two to three years eat the equivalent of an adult female (van Orsdol 1982) and large cubs eat 0.75 times that of adult lionesses (Schaller 1972; van Orsdol 1982, 1986). Large cubs were defined as lions between the ages of one and two years

(Schaller 1972; Smuts *et al.* 1978; Stander 1991). Small cubs of less than one year were assumed to require one third as much food as an adult female (Packer *et al.* 1990). Daily food intake was measured per Female Equivalent Unit or FEQ (Bertram 1979; Packer *et al.* 1994), assuming that carcasses were divided equally among the lions at a kill. This is supported by the fact that both northern and southern prides are small and there is no dominance hierarchy among lionesses when feeding and as a result, the competition for food resources within prides is likely to be low (Schaller 1972; Packer & Pusey 1983; Stander 1992; Hunter 1998). The FEQ for cubs was adjusted according to the proportion of the year that they spent as small or large cubs.

The daily intake rates (kg/FEQ/day) calculated from all the kills recorded over the study period were biased by a number of long periods between sightings. For example, the longest gap between consecutive sightings of the same group of animals was 97 days. Therefore, a second calculation was made using only kills made by the same groups of animals and within five days of each other for years 1 to 3. Where buffalo numbers in the lions' diet are minimal, the interval between kills is reported to vary from 15 to 32 kills per lion per year or 2.4 to 11.4 days between kills for a single lion (see Saba 1979). Given that each pride consists of two lionesses, the primary hunters, the maximum interval between kills should be 5.7 days. Since more than half the kills made by both prides were within five days of each and taking into account the presence of pride males and cubs which would decrease the interval between kills due to minimum daily intake requirements, five days was chosen as the maximum interval and was viewed as a conservative estimate. There should be fewer missed kills in this subset of the data, which should therefore be more robust than the full set and give a better picture of the diet of the lions. All calculations were repeated for the full and subset of data. When calculating daily intake rates for the subset of data, kills made on the same day were divided by a factor of 0.5 to indicate half a day. Seasonal variation in daily intake rates could not be calculated because the fluctuations in the tourist numbers, and therefore the observation effort, created problems of unequal and often small sample sizes when analyzing the data seasonally. In addition, management decisions, in general, are made on an annual basis and therefore do not require detailed seasonal reports.

*Calculation of annual offtake*

The annual offtake (ungulates removed by lions) was calculated in terms of biomass consumed and numbers killed. The observed values from the full data set and the subset were compared with values calculated using a method based on the formula proposed by Goodman (unpub. report & pers. comm., Natal Parks Board, 2002), which was used to calculate how many individuals per species should be culled annually in a small reserve with no large predators, in order to simulate natural offtake. This formula assumes that lions hunt prey species according to their relative abundances on the reserve:

$$\mathrm{E_x} = \frac{\mathrm{N_x}}{\mathrm{N_t}} \times E_t$$

where $E_x$ is the estimated number of species x falling prey to lions. $N_x$ is the estimated number of prey species x in the population $N_t$ which is the population estimate of all prey likely to be consumed by lions. The prey likely to be consumed by lions was not restricted to their preferred mass range since lions will opportunistically hunt small species such as duiker and bushbuck during the day (van Orsdol 1984), and since all species should be considered in the management of the reserve. $E_t$ is the estimated total number of prey animals to be removed. Whereas Goodman's formula uses a kill rate constant of 25kg/kg predator/year and estimates the number of lions which would naturally be present using the equations proposed by East (1984), in this study the number of lions was known and the daily intake rate could be calculated, therefore $E_t$ was derived using the formula:

$$\mathrm{E_t} = \frac{\text{daily intake} \times \text{no. of lions} \times \text{no.of days}}{\text{weighted mean mass of prey}}$$

The daily intake rates were taken from the literature, and two calculations of estimated offtake were made using Schaller's (1972) estimate of 5kg per female per day and an average value of 7.12kg per female per day derived from nine studies of lion populations in different areas (see Appendix 1). Schaller's (1972) estimate is often used for comparison, and was therefore included to provide comparison between this study and previous estimates. The average of 7.12kg was used because many studies have found that the daily intake rate per FEQ was greater than that found by Schaller (1972). The number of lions was calculated as the number of FEQs present on the reserve during the time period analysed. The weighted mean mass of prey was calculated as the total biomass of the populations of prey selected by lions over the study period (excluding predators and species for which populations estimates were not available), divided by the total number of prey animals on the reserve. For the subset of data, the number of days used in the calculation was considered to be the number of days in each year for which there were reliable data (kills observed within five days of each other). Comparisons were therefore made on a yearly basis, between the subset of data for a particular year and the estimated number of kills that would have been made in the same number of days in that year using the Goodman equation. In addition, the total subset of data was compared to an estimate derived using the average prey biomass available in the three years, the average number of lions on the reserve over the study period and 368.5 days of observation.

Differences between observed and estimated offtake were not compared statistically because of the known error in the observed values which would make any statistically significant differences difficult to interpret.

## RESULTS

The subset of the full set of data comprised 232 animals killed over a period of 368.5 days that included periods ranging in length from 31 days, during which 15 animals were killed, to a single day, during which two animals were killed.

A total of 25 species were preyed on in Shamwari over the study period (Table 3.2) while only 18 species were recorded from the subset of data (Table 3.3). The seven species not included in the subset were porcupine (3), brown hyena (1), Egyptian goose (1), jackal (1), vervet monkey (1) and cheetah (1). These species made up only 2.2% of the total number of animals preyed on (Table 3.2) and, apart from the porcupine, they were all killed and then abandoned without feeding. The number of kills in the subset represented 64.8% of the total observed kills in terms of numbers and 66.3% in terms of biomass while the duration of the subset was only 33.6% of the study period. A comparison of the two data sets indicated that each species was preyed on in about the same proportion, and percentages were never more than 2.5% different (compare Tables 3.2 and 3.3). A similar result was found for biomass consumption, where the difference between the total observed kills and the subset of data was never greater than 3.4% for any species (compare Tables 3.2 and 3.3). For the full data set, five species (kudu, black wildebeest, warthog, bushbuck and blesbuck) comprised 206 (67.9%) of the number of animals killed and 24690.3kg (67.8%) of the total biomass. The top five species killed by lions were the same in the subset of data and comprised 161 (69.5%) of the number of animals killed and 16758.5kg (65.6%) of the total biomass. In both data sets, the top two species were animals belonging to the large size class and kudu formed a far greater proportion of the diet (31.9% and 29.5%) than any other species (Tables 3.2 and 3.3).

In terms of size, more than half of the kills recorded over the study period were of the large size class (Figure 3.1). When the subset of data was analysed, there were only minor differences between the two data sets (compare Figures 3.1 and 3.2).

The number of kills where the age (Figure 3.3) and/or sex (Figure 3.4) was not known or not recorded was high for both the full and subset of data. In species such as zebra and blesbuck the sex of animals is difficult to determine and was seldom recorded. In cases where the age was not recorded it is likely that the animal was adult but the assumption was not made when analyzing the data to avoid errors. For both data sets, more males were killed than females and the majority of animals were adults (Figure 3.3 & 3.4). The relative abundances of males and females, and the age classes within populations is not known and it is therefore not possible to establish whether the lions preyed on the age classes or sexes according to their abundances.

Table 3.2. Number and total edible biomass of prey species killed by lions on Shamwari between October 2001 and September 2003.

| | Kills | | Biomass[1] | |
|---|---|---|---|---|
| Species | Number | % | kg | % |
| Kudu | 106 | 29.5 | 15900.0 | 41.4 |
| Wildebeest (black) | 42 | 11.7 | 4816.0 | 16.1 |
| Warthog | 38 | 10.6 | 1995.0 | 5.2 |
| Bushbuck | 31 | 8.6 | 744.0 | 1.9 |
| Blesbuck | 27 | 7.5 | 1235.3 | 3.2 |
| Eland | 19 | 5.3 | 6175.0 | 16.1 |
| Red hartebeest | 16 | 4.5 | 1440.0 | 3.8 |
| Ostrich | 15 | 4.2 | 772.9 | 2.0 |
| Duiker | 13 | 3.6 | 197.6 | 0.5 |
| Impala | 10 | 2.8 | 400.0 | 1.0 |
| Zebra | 8 | 2.2 | 1352.0 | 3.5 |
| Gemsbok | 7 | 2.0 | 1102.5 | 2.9 |
| Springbuck | 5 | 1.4 | 148.0 | 0.4 |
| Wildebeest (blue) | 4 | 1.1 | 504.0 | 1.3 |
| Waterbuck | 4 | 1.1 | 504.0 | 1.3 |
| Porcupine | 3 | 0.8 | | |
| Giraffe | 2 | 0.6 | 1079.0 | 2.8 |
| Mountain reedbuck | 2 | 0.6 | 48.0 | 0.1 |
| Brown hyena | 1 | 0.3 | | |
| Egyptian goose | 1 | 0.3 | | |
| Jackal | 1 | 0.3 | | |
| Monitor lizard | 1 | 0.3 | | |
| Springbuck (black) | 1 | 0.3 | 29.6 | 0.1 |
| Vervet monkey | 1 | 0.3 | | |
| Cheetah | 1 | 0.3 | | |
| Total | 358 | 100 | 38442.8 | 100 |

[1] from van Rooyen *et al.* (1996)

Table 3.3. Number and total edible biomass of prey species killed by lions on Shamwari between October 2001 and September 2003 calculated from the subset of data.

| | Kills | | Biomass | |
|---|---|---|---|---|
| Species | Number | % | kg | % |
| Kudu | 74 | 31.9 | 11100.0 | 43.5 |
| Wildebeest (black) | 29 | 12.5 | 3248.0 | 12.7 |
| Warthog | 22 | 9.5 | 1155.0 | 4.5 |
| Blesbuck | 18 | 7.8 | 823.5 | 3.2 |
| Bushbuck | 18 | 7.8 | 432.0 | 1.7 |
| Red hartebeest | 14 | 6.0 | 1260.0 | 4.9 |
| Eland | 11 | 4.7 | 3575.0 | 14.0 |
| Ostrich | 10 | 4.3 | 515.3 | 2.0 |
| Duiker | 10 | 4.3 | 152.0 | 0.6 |
| Zebra | 6 | 2.6 | 1014.0 | 4.0 |
| Gemsbok | 4 | 1.7 | 630.0 | 2.5 |
| Waterbuck | 4 | 1.7 | 504.0 | 2.0 |
| Impala | 4 | 1.7 | 160.0 | 0.6 |
| Springbuck | 3 | 1.3 | 88.8 | 0.3 |
| Wildebeest (blue) | 2 | 0.9 | 252.0 | 1.0 |
| Giraffe | 1 | 0.4 | 539.5 | 2.1 |
| Springbuck (black) | 1 | 0.4 | 29.6 | 0.1 |
| Mountain reedbuck | 1 | 0.4 | 24.0 | 0.1 |
| Total | 232 | 100 | 25502.7 | 100.0 |

[1] from van Rooyen *et al.* (1996)

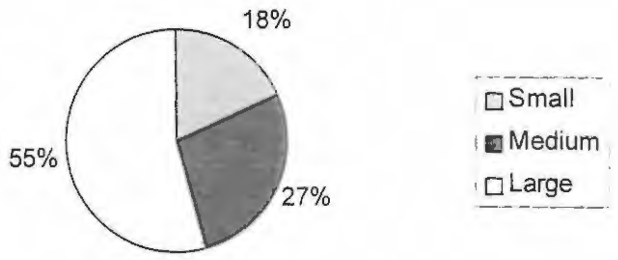

Figure 3.1. Proportion of small, medium and large animals found in the diet of lions at Shamwari from October 2000 to September 2003.

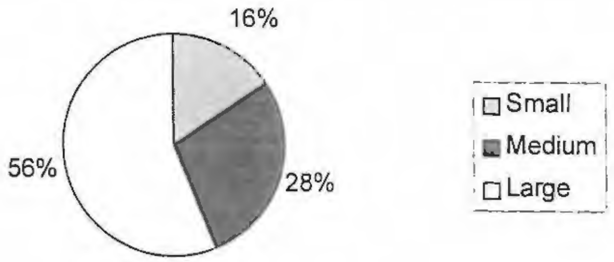

Figure 3.2. Proportion of small, medium and large animals found in the diet of lions at Shamwari, using the subset of kills.

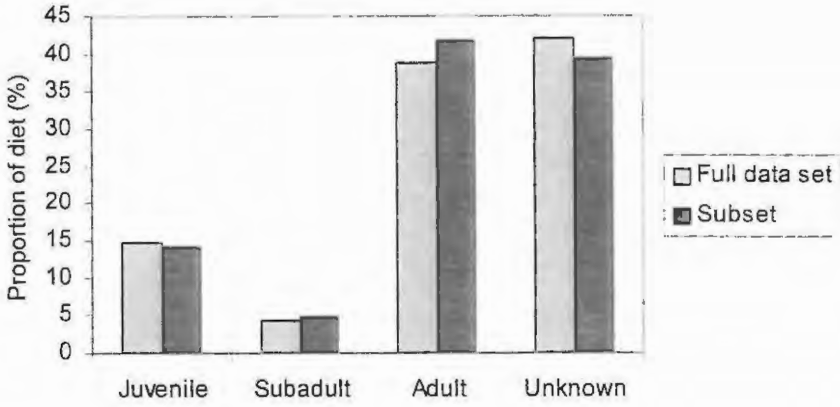

Figure 3.3. Proportion of each age class selected by lions for all species on both reserves.

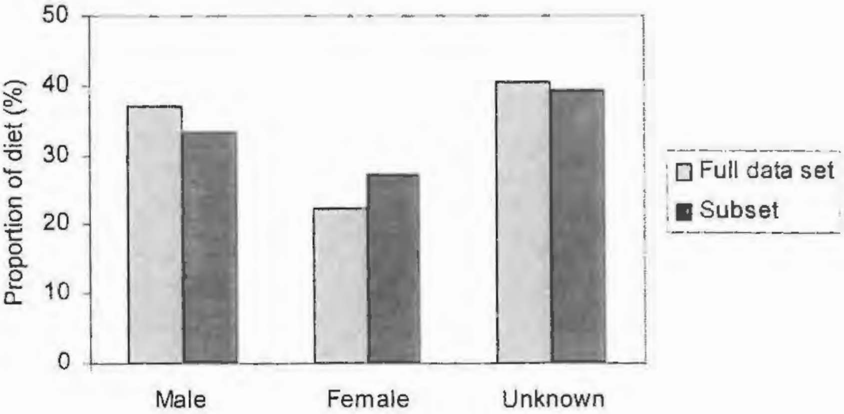

Figure 3.4. Proportion of males, females and animals of unknown sex selected by lions for all species on both reserves.

### *Prey preference*

The calculation of prey preference indices for the full data set (see Appendix C Table 1) has generated values from a maximum of 10.32 in year 3 for black wildebeest to minima of 0.00 for giraffe in year 1 and 0.08 for grey duiker in year 3 (Table 3.4). In this analysis, I have interpreted values below 1 as indicating avoidance, values between 1 and 2 as indicating that the prey is being utilized according to abundance, and values greater than 2 as indicating a preference for a particular species. Prey preference indices have been calculated using both data sets and the only noteworthy differences between the overall preference indices calculated from the two data sets for each species (Tables 3.4 & 3.5; see Appendix C Tables 1 & 2 for calculations) were changes in preference 'categories' for waterbuck (0.86 and 1.33), giraffe (1.53 and 2.42) and red hartebeest (1.63 and 2.20), although the differences in the actual values were very small. There were, however, substantial differences in preference ratings between the full and subset of data for year 3 for waterbuck (2.77 and 5.53), red hartebeest (2.18 and 4.37), eland (1.84 and 0.00), warthog (4.97 and 3.11), ostrich (2.72 and 5.45) and black wildebeest (10.32 and 6.35). In terms of preference ratings, kudu, which was the most common prey item, was selected according to its relative abundances in both data sets. The preference indices for warthog, ostrich and wildebeest were relatively high although preference for ostrich decreased substantially after year 1. Wildebeest preference decreased after year 1 but increased again in year 2, and warthog on the other hand were most strongly favoured in year 2. All the species with the lowest preference indices on Shamwari were those that fall within the small size class

Table 3.4. The preference indices for species killed by lions on Shamwari for each year of the study period and the overall preference indices, using the full data set. Size is Small (S), Medium (M) or Large (L) as in Table 3.1.

| Species | Year 1 | Year 2 | Year 3 | Overall | Size |
|---|---|---|---|---|---|
| Mountain Reedbuck | 0.24 | 0.00 | 0.00 | 0.08 | S |
| Impala | 0.10 | 0.24 | 0.27 | 0.19 | S |
| Duiker | 0.08 | 0.32 | 0.20 | 0.20 | S |
| Springbuck | 0.14 | 0.50 | 0.37 | 0.33 | S |
| Bushbuck | 0.38 | 0.73 | 0.30 | 0.49 | S |
| Waterbuck | 0.55 | 0.00 | 2.77 | 0.86 | L |
| Blesbuck | 2.12 | 0.75 | 0.47 | 1.26 | M |
| Zebra | 1.71 | 1.82 | 0.00 | 1.27 | L |
| Giraffe | 0.00 | 4.28 | 0.00 | 1.53 | L |
| Red Hartebeest | 1.64 | 1.25 | 2.18 | 1.63 | M |
| Gemsbok | 1.77 | 1.79 | 1.06 | 1.65 | L |
| Kudu | 1.49 | 1.91 | 1.97 | 1.76 | L |
| Eland | 2.74 | 2.64 | 1.84 | 2.55 | L |
| Warthog | 1.66 | 9.21 | 4.97 | 4.86 | M |
| Ostrich | 10.29 | 1.77 | 2.72 | 5.92 | M |
| Wildebeest (black) | 9.39 | 1.70 | 10.32 | 6.12 | L |

Table 3.5. The preference indices for species killed by lions on Shamwari for each year of the study period and the overall preference indices calculated from the subset of data.

| Species | Year 1 | Year 2 | Year 3 | Overall | Size |
|---|---|---|---|---|---|
| Mountain reedbuck | 0.18 | 0.00 | 0.00 | 0.06 | S |
| Impala | 0.08 | 0.09 | 0.13 | 0.09 | S |
| Duiker | 0.06 | 0.40 | 0.27 | 0.24 | S |
| Springbuck | 0.00 | 0.47 | 0.75 | 0.31 | S |
| Bushbuck | 0.42 | 0.57 | 0.24 | 0.44 | S |
| Zebra | 1.25 | 1.93 | 0.00 | 1.22 | L |
| Blesbuck | 2.07 | 0.76 | 0.47 | 1.30 | M |
| Waterbuck | 0.81 | 0.00 | 5.53 | 1.33 | L |
| Gemsbok | 0.86 | 1.69 | 2.12 | 1.46 | L |
| Kudu | 1.64 | 1.93 | 2.29 | 1.87 | L |
| Red hartebeest | 1.59 | 1.77 | 4.37 | 2.20 | M |
| Eland | 3.00 | 2.34 | 0.00 | 2.29 | L |
| Giraffe | 0.00 | 6.05 | 0.00 | 2.42 | L |
| Warthog | 1.62 | 10.29 | 3.11 | 4.35 | M |
| Wildebeest (black) | 9.72 | 1.61 | 6.35 | 5.49 | L |
| Ostrich | 10.02 | 2.51 | 5.45 | 6.78 | M |

***Interval between kills (kill rate)***

The intervals between recorded kills were similar for both prides (Figure 3.5). The long tail to the right of Figure 3.5 is clear evidence that many kills were missed and it is for this reason that data analyses have been done for the full data set and the subset. The average interval between kills for the full data set was 2.8, 2.7 and 4.2 days for years 1, 2 and 3 respectively while the averages for the subset of data (both prides combined) was lower, with 1.4, 1.6 and 2.0 days between kills for years 1, 2 and 3 respectively.

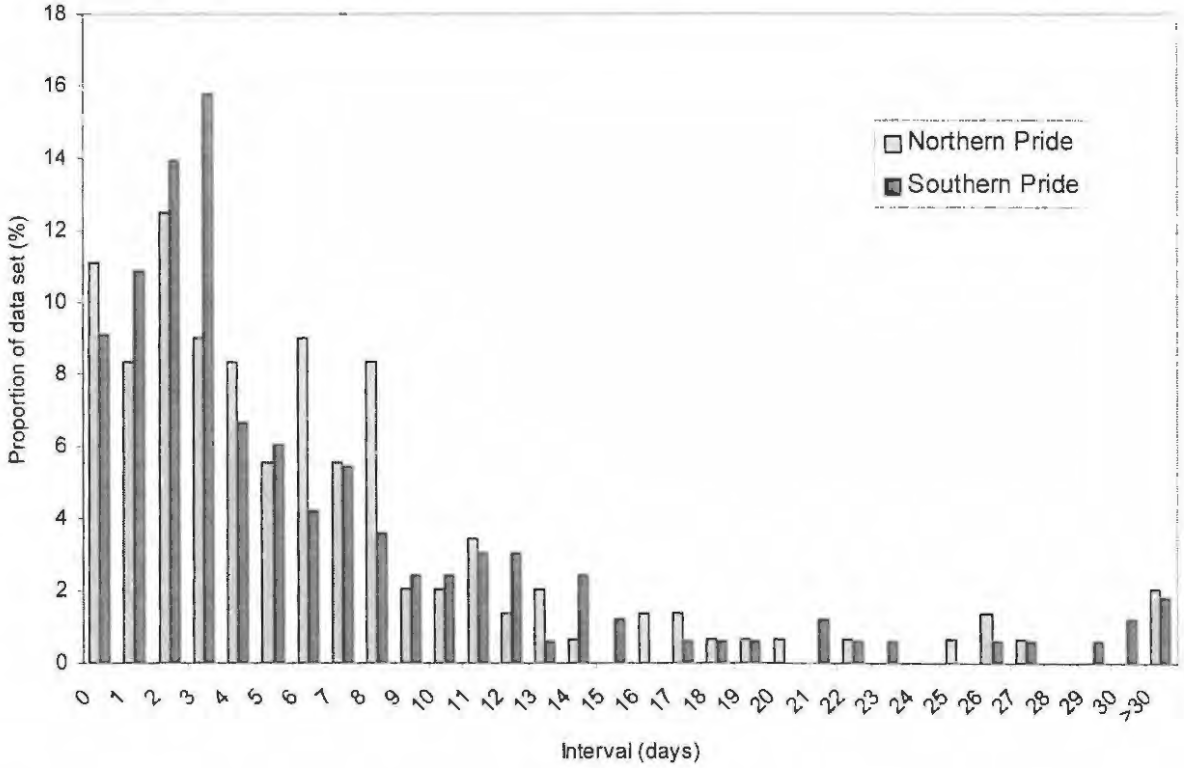

Figure 3.5. The frequency of occurrence of intervals between kills made between October 2000 and September 2003 for the two prides on Shamwari.

### *Calculation of daily intake rates*

The average daily intake rate per FEQ (kg.day$^{-1}$) was calculated separately for the two data sets and for the three years for which data were available (Tables 3.6 & 3.7). For both data sets, the average daily intake decreased from year one to year three and values were substantially lower for the full data set than for the subset.

The average daily intake rates calculated from the full data set of all kills (Table 3.6) were close to Schaller's (1979) estimate of 5kg/FEQ/day for the first two years but very low for the third year. The third year only approached 5kg/FEQ/year when the daily intake rate was calculated from the subset of data and the intake rates calculated for the first two years were almost double the estimates from the full data set (Table 3.7).

Table 3.6. Daily intake rates from Shamwari, using the full set of the data

| | Edible biomass | Kills | | | Biomass (kg) | | |
|---|---|---|---|---|---|---|---|
| Species | (kg)[1] | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 |
| Blesbuck | 45.8 | 18 | 7 | 2 | 823.5 | 320.3 | 91.5 |
| Bushbuck | 24.0 | 8 | 18 | 5 | 192.0 | 432.0 | 120.0 |
| Duiker | 15.2 | 2 | 8 | 3 | 30.4 | 121.6 | 45.6 |
| Eland | 325.0 | 8 | 8 | 3 | 2600.0 | 2600.0 | 975.0 |
| Gemsbok | 157.5 | 3 | 3 | 1 | 472.5 | 472.5 | 157.5 |
| Giraffe | 539.5 | 0 | 2 | 0 | 0.0 | 1079.0 | 0.0 |
| Impala | 40.0 | 2 | 4 | 4 | 80.0 | 160.0 | 160.0 |
| Kudu | 150.0 | 33 | 42 | 31 | 4950.0 | 6300.0 | 4650.0 |
| Mountain reedbuck | 24.0 | 2 | 0 | 0 | 48.0 | 0.0 | 0.0 |
| Ostrich | 51.5 | 12 | 2 | 1 | 618.3 | 103.1 | 51.5 |
| Red hartebeest | 90.0 | 6 | 5 | 5 | 540.0 | 450.0 | 450.0 |
| Springbuck | 29.6 | 1 | 3 | 1 | 29.6 | 88.8 | 29.6 |
| Springbuck (black) | 29.6 | 1 | 0 | 0 | 29.6 | 0.0 | 0.0 |
| Warthog | 52.5 | 3 | 19 | 16 | 157.5 | 997.5 | 840.0 |
| Waterbuck | 126.0 | 1 | 0 | 3 | 126.0 | 0.0 | 378.0 |
| Wildebeest | 112.0 | 24 | 6 | 13 | 2688.0 | 672.0 | 1456.0 |
| Wildebeest (blue) | 126.0 | 2 | 2 | 0 | 252.0 | 252.0 | 0.0 |
| Zebra | 169.0 | 4 | 4 | 0 | 676.0 | 676.0 | 0.0 |
| Total | | 130 | 133 | 88 | 14313.4 | 14724.7 | 9404.7 |
| No. of FEQ[2] | | | | | 7.50 | 8.54 | 11.39 |
| Daily intake | = total biomass/no. of FEQ/365 | | | | 5.23 | 4.72 | 2.26 |

[1] Calculated following Viljoen (1997)

[2] See Methods for detailed calculations

Table 3.7. Daily intake rates from Shamwari, using the subset of the data

| | Edible biomass | Kills | | | Biomass eaten (kg) | | |
|---|---|---|---|---|---|---|---|
| Species | (kg)[1] | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 |
| Blesbuck | 45.8 | 12 | 5 | 1 | 549.0 | 228.8 | 45.8 |
| Bushbuck | 24.0 | 6 | 10 | 2 | 144.0 | 240.0 | 48.0 |
| Duiker | 15.2 | 1 | 7 | 2 | 15.2 | 106.4 | 30.4 |
| Eland | 325.0 | 6 | 5 | 0 | 1950.0 | 1625.0 | 0.0 |
| Gemsbok | 157.5 | 1 | 2 | 1 | 157.5 | 315.0 | 157.5 |
| Giraffe | 539.5 | 0 | 2 | 0 | 0.0 | 1079.0 | 0.0 |
| Impala | 40.0 | 1 | 1 | 1 | 40.0 | 40.0 | 40.0 |
| Kudu | 150.0 | 25 | 30 | 18 | 3750.0 | 4500.0 | 2700.0 |
| Mountain reedbuck | 24.0 | 1 | 0 | 0 | 24.0 | 0.0 | 0.0 |
| Ostrich | 51.5 | 8 | 2 | 1 | 412.2 | 103.1 | 51.5 |
| Red hartebeest | 90.0 | 4 | 5 | 5 | 360.0 | 450.0 | 450.0 |
| Springbuck | 29.6 | 0 | 2 | 1 | 0.0 | 59.2 | 29.6 |
| Springbuck (black) | 29.6 | 1 | 0 | 0 | 29.6 | 0.0 | 0.0 |
| Warthog | 52.5 | 2 | 15 | 5 | 105.0 | 787.5 | 262.5 |
| Waterbuck | 126.0 | 1 | 0 | 3 | 126.0 | 0.0 | 378.0 |
| Wildebeest | 112.0 | 17 | 4 | 4 | 1904.0 | 448.0 | 448.0 |
| Wildebeest (blue) | 126.0 | 1 | 1 | 0 | 126.0 | 126.0 | 0.0 |
| Zebra | 169.0 | 2 | 3 | 0 | 338.0 | 507.0 | 0.0 |
| Total | | 89 | 94 | 44 | 10030.5 | 10614.9 | 4641.3 |
| No.of FEQ[2] | | | | | 7.50 | 8.54 | 11.39 |
| Days in subset | = total days in subset of original data | | | | 128.0 | 150.5 | 90.0 |
| Daily intake | = total biomass eaten/no. of FEQ/days | | | | 10.45 | 8.25 | 4.53 |

[1] Calculated following Viljoen (1997)

[2] See Methods for detailed calculations

### *Calculation of annual offtake*

Goodman's formula was used to calculate estimated predation on each of the prey species and Table 8 shows a specimen set of calculations. Calculations were made using daily intake rate of 5kg/FEQ (Schaller 1972) and 7.12kg/FEQ for both the full (Tables 3.9 & 3.10) and subset of data (Tables 3.11 & 3.12).

The total number of kills observed throughout the study period (full data set) was less than estimated using Goodman's formula and the differences were greater than 37% for all years using both daily intake rates (Tables 3.9 & 3.10). For the subset of data, the second year of the subset was very similar (4% difference) to the total estimated kills for that year when a daily intake of 5kg/FEQ/day was used (Table 3.11). When the intake rate of 7.12kg/FEQ/day was used in the formula (Table 3.12), there was only a 13% difference between the estimated and observed values for year 1. The third years' results did not correspond to either calculation. The total number of kills recorded for all years of the subset was closer to Schaller's (1972) estimate (Table 3.11) than to the average intake rate of 7.12kg/FEQ/day. At a species level, the pattern of differences between observed and expected predation rates is more complex. Using the subset of data only, there were five species (blesbuck, ostrich, red hartebeest, warthog, and black wildebeest) which had positive differences between observed and expected predation rates for both intake rates (i.e. more of the species were killed than was estimated by Goodman's formula; Tables 3.11 & 3.12). Blesbuck and red hartebeest had small differences but the differences for ostrich warthog and black wildebeest were much larger. Bushbuck had one negative and one positive difference, although these were both relatively small. The remainder of species were killed less than was estimated with negative differences ranging from relatively small differences for duiker and kudu, to much greater differences for impala and mountain reedbuck.

Table 3.8. A "specimen" calculation of estimated removal of prey using Goodman's formula $E_x = \frac{N_x}{N_t} \times E_t$ where $E_t = \frac{\text{daily intake} \times \text{no. of lions} \times 365}{\text{weighted mean mass of prey}}$

| Species | Mass | Counts | Biomass | Estimated removals | Kills observed[1] | Differences[2] (%) |
|---|---|---|---|---|---|---|
| Blesbuck | 45.75 | 305 | 13954 | 13 | 18 | 38 |
| Bushbuck | 24 | 750 | 18000 | 33 | 8 | -76 |
| Duiker | 15.2 | 900 | 13680 | 39 | 2 | -95 |
| Eland | 325 | 105 | 34125 | 5 | 8 | 60 |
| Gemsbok | 157.5 | 61 | 9608 | 3 | 3 | 0 |
| Giraffe | 539.5 | 18 | 9711 | 1 | 0 | -100 |
| Impala | 40 | 694 | 27760 | 30 | 2 | -93 |
| Kudu | 150 | 800 | 120000 | 35 | 33 | -6 |
| Mountain reedbuck | 24 | 300 | 7200 | 13 | 2 | -85 |
| Ostrich | 56.25 | 42 | 2363 | 2 | 12 | 500 |
| Red hartebeest | 90 | 132 | 11880 | 6 | 6 | 0 |
| Springbuck | 29.6 | 257 | 7607 | 11 | 1 | -91 |
| Springbuck (black) | 29.6 | 7 | 207 | 0 | 1 | - |
| Warthog | 52.5 | 65 | 3413 | 3 | 3 | 0 |
| Waterbuck | 126 | 65 | 8190 | 3 | 1 | -67 |
| Wildebeest | 112 | 92 | 10304 | 4 | 24 | 500 |
| Wildebeest (blue) | 126 | 3 | 378 | 0 | 2 | - |
| Zebra | 169 | 84 | 14196 | 4 | 4 | 0 |
| Total | 2111.9 | 4680 | 312575 | 205 | 130 | -37 |

CALCULATIONS:

| | | |
|---|---|---|
| Weighted mean mass | = total biomass/total count | 66.79 |
| No. of FEQs in population[3] | | 7.495 |
| Daily intake (kg/FEQ/day) | = Schallers' (1972) estimate | 5 |
| kg required (per year) | = no. of FEQs x daily intake x 365 | 13678.38 |
| Estimated total no. prey removed | = kg required/weighted mean mass (rounded off) | 205 |
| Estimated no. per spp | = spp count/total count x estimated total no. of prey<br>blesbuck example: 305/4680 x 205 (rounded off) | |

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[1] These are the total kills observed through opportunistic observations by rangers per species for the time period being analysed (i.e. a particular year).

[2] The differences are calculated as observed kills as a percentages of estimated kills and then a factor of 100 is subtracted from each to give positive and negative percentages which illustrates the relative increase and decrease, respectively, of the observed kills from the estimated removal.

[3] See Methods for calculation.

Table 3.9. Kills observed on Shamwari for each year between October 2000 and September 2003 compared to the estimated kills obtained from Goodman's formula using a daily intake rate for lions of 5 kg/FEQ/day. The differences are calculated as the percentage variation of the observed from the estimated.

| | Observed kills | | | Estimated removal | | | Differences (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 |
| Blesbuck | 18 | 7 | 2 | 13 | 17 | 15 | 38 | -59 | -87 |
| Bushbuck | 8 | 18 | 5 | 33 | 44 | 59 | -76 | -59 | -92 |
| Duiker | 2 | 8 | 3 | 39 | 44 | 53 | -95 | -82 | -94 |
| Eland | 8 | 8 | 3 | 5 | 5 | 6 | 60 | 60 | -50 |
| Gemsbok | 3 | 3 | 1 | 3 | 3 | 3 | 0 | 0 | -67 |
| Giraffe | 0 | 2 | 0 | 1 | 1 | 1 | -100 | 100 | -100 |
| Impala | 2 | 4 | 4 | 30 | 29 | 53 | -93 | -86 | -92 |
| Kudu | 33 | 42 | 31 | 35 | 39 | 56 | -6 | 8 | -45 |
| Mountain reedbuck | 2 | 0 | 0 | 13 | 17 | 22 | -85 | -100 | -100 |
| Ostrich | 12 | 2 | 1 | 2 | 2 | 1 | 500 | 0 | 0 |
| Red hartebeest | 6 | 5 | 5 | 6 | 7 | 8 | 0 | -29 | -38 |
| Springbuck | 1 | 3 | 1 | 11 | 11 | 10 | -91 | -73 | -90 |
| Springbuck (black) | 1 | 0 | 0 | 0 | 0 | 0 | - | - | - |
| Warthog | 3 | 19 | 16 | 3 | 4 | 12 | 0 | 375 | 33 |
| Waterbuck | 1 | 0 | 3 | 1 | 3 | 4 | -67 | -100 | -25 |
| Wildebeest (black) | 24 | 6 | 13 | 4 | 6 | 5 | 500 | 0 | 160 |
| Wildebeest (blue) | 2 | 2 | 0 | 0 | 0 | 0 | - | - | - |
| Zebra | 4 | 4 | 0 | 4 | 4 | 6 | 0 | 0 | -100 |
| Total | 130 | 133 | 88 | 205 | 236 | 314 | -37 | -44 | -72 |

Table 3.10. Kills observed on Shamwari for each year between October 2000 and September 2003 compared to the estimated kills obtained from Goodman's formula using a daily intake rate for lions of 7.12 kg/FEQ/day. The differences are calculated as the percentage variation of the observed from the estimated.

| | Observed kills | | | Estimated removal | | | Differences | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 |
| Blesbuck | 18 | 7 | 2 | 19 | 24 | 22 | -5 | -71 | -91 |
| Bushbuck | 8 | 18 | 5 | 47 | 62 | 85 | -83 | -71 | -94 |
| Duiker | 2 | 8 | 3 | 56 | 62 | 76 | -96 | -87 | -96 |
| Eland | 8 | 8 | 3 | 7 | 8 | 8 | 14 | 0 | -63 |
| Gemsbok | 3 | 3 | 1 | 4 | 4 | 5 | -25 | -25 | -80 |
| Giraffe | 0 | 2 | 0 | 1 | 1 | 2 | -100 | 100 | -100 |
| Impala | 2 | 4 | 4 | 43 | 42 | 76 | -95 | -90 | -95 |
| Kudu | 33 | 42 | 31 | 50 | 56 | 80 | -34 | -25 | -61 |
| Mountain reedbuck | 2 | 0 | 0 | 19 | 24 | 31 | -89 | -100 | -100 |
| Ostrich | 12 | 2 | 1 | 3 | 3 | 2 | 300 | -33 | -50 |
| Red hartebeest | 6 | 5 | 5 | 8 | 10 | 12 | -25 | -50 | -58 |
| Springbuck | 1 | 3 | 1 | 16 | 15 | 14 | -94 | -80 | -93 |
| Springbuck (black) | 1 | 0 | 0 | 1 | 0 | 0 | - | - | - |
| Warthog | 3 | 19 | 16 | 4 | 5 | 16 | -25 | 280 | 0 |
| Waterbuck | 1 | 0 | 3 | 4 | 5 | 6 | -75 | -100 | -50 |
| Wildebeest (black) | 24 | 6 | 13 | 6 | 9 | 6 | 300 | -33 | 117 |
| Wildebeest (blue) | 2 | 2 | 0 | 0 | 0 | 0 | - | - | - |
| Zebra | 4 | 4 | 0 | 5 | 6 | 9 | -20 | -33 | -100 |
| Total | 130 | 133 | 88 | 292 | 336 | 450 | -55 | -60 | -80 |

Table 3.11. Kills observed on Shamwari within five days of each other for each year between October 2000 and September 2003 and the total for all years compared to the estimated kills obtained from Goodman's formula using a daily intake rate for lions of 5 kg/FEQ/day for the number of days in each year of the subset of data. The differences are calculated as the percentage variation of the observed from the estimated.

| | Kills | | | | Estimated removal | | | | Differences (%) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Year 1 | Year 2 | Year 3 | All years | Year 1 | Year 2 | Year 3 | All years | Year 1 | Year 2 | Year 3 | All years |
| Blesbuck | 12 | 5 | 1 | 18 | 3 | 5 | 3 | 11 | 300 | 0 | -67 | 64 |
| Bushbuck | 6 | 10 | 2 | 18 | 4 | 7 | 5 | 16 | 50 | 43 | -60 | 13 |
| Duiker | 1 | 7 | 2 | 10 | 3 | 4 | 3 | 11 | -67 | 75 | -33 | -9 |
| Eland | 6 | 5 | 0 | 11 | 8 | 11 | 7 | 26 | -25 | -55 | -100 | -31 |
| Gemsbok | 1 | 2 | 1 | 4 | 2 | 3 | 2 | 7 | -50 | -33 | -50 | -43 |
| Giraffe | 0 | 2 | 0 | 2 | 2 | 3 | 2 | 8 | -100 | -33 | -100 | -75 |
| Impala | 1 | 1 | 1 | 3 | 6 | 7 | 8 | 23 | -83 | -86 | -88 | -87 |
| Kudu | 25 | 30 | 18 | 73 | 28 | 36 | 32 | 99 | -11 | -17 | -44 | -26 |
| Mountain reedbuck | 1 | 0 | 0 | 1 | 2 | 3 | 2 | 6 | -50 | -100 | -100 | -83 |
| Ostrich | 8 | 2 | 1 | 11 | 1 | 1 | 0 | 2 | 700 | 100 | - | 450 |
| Red hartebeest | 4 | 5 | 5 | 14 | 3 | 4 | 3 | 10 | 33 | 25 | 67 | 40 |
| Springbuck | 0 | 2 | 1 | 3 | 2 | 2 | 1 | 5 | -100 | 0 | 0 | -40 |
| Springbuck (black) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | 0 | - | 0 |
| Warthog | 2 | 15 | 5 | 22 | 1 | 1 | 2 | 4 | 100 | 1400 | 150 | 450 |
| Waterbuck | 1 | 0 | 3 | 4 | 2 | 2 | 2 | 6 | -50 | -100 | 50 | -33 |
| Wildebeest (black) | 17 | 4 | 4 | 25 | 2 | 4 | 2 | 9 | 750 | 0 | 100 | 178 |
| Wildebeest (blue) | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | - | - | 0 | - |
| Zebra | 2 | 3 | 0 | 5 | 3 | 4 | 4 | 12 | -33 | -25 | -100 | -58 |
| Total kills | 89 | 94 | 44 | 227 | 72 | 97 | 78 | 254 | 24 | -3 | -44 | -11 |
| Days in subsample | 128.0 | 150.5 | 90.0 | 368.5 | | | | | | | | |
| No. of lions | 7.5 | 8.3 | 11.4 | 9.1 | | | | | | | | |

Table 3.12. Kills observed on Shamwari within five days of each other for each year between October 2000 and September 2003 and the total for all years compared to the estimated kills obtained from Goodman's formula using a daily intake rate for lions of 7.12 kg/FEQ/day for the number of days in each year of the subset of data. The differences are calculated as the percentage variation of the observed from the estimated.

| | Kills | | | | Estimated removal | | | | Differences (%) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Year 1 | Year 2 | Year 3 | All Years | Year 1 | Year 2 | Year 3 | All years | Year 1 | Year 2 | Year 3 | All years |
| Blesbuck | 12 | 5 | 1 | 18 | 5 | 7 | 4 | 16 | 140 | -29 | -75 | 13 |
| Bushbuck | 6 | 10 | 2 | 18 | 6 | 9 | 8 | 24 | 0 | 11 | -75 | -25 |
| Duiker | 1 | 7 | 2 | 10 | 4 | 6 | 4 | 16 | -75 | 17 | -50 | -38 |
| Eland | 6 | 5 | 0 | 11 | 11 | 15 | 10 | 39 | -45 | -67 | -100 | -72 |
| Gemsbok | 1 | 2 | 1 | 4 | 3 | 4 | 3 | 11 | -67 | -50 | -67 | -64 |
| Giraffe | 0 | 2 | 0 | 2 | 3 | 4 | 3 | 11 | -100 | -50 | -100 | -82 |
| Impala | 1 | 1 | 1 | 3 | 9 | 10 | 11 | 33 | -89 | -90 | -91 | -91 |
| Kudu | 25 | 30 | 18 | 73 | 39 | 52 | 45 | 146 | -36 | -42 | -60 | -50 |
| Mountain reedbuck | 1 | 0 | 0 | 1 | 2 | 4 | 3 | 9 | -50 | -100 | -100 | -89 |
| Ostrich | 8 | 2 | 1 | 11 | 1 | 1 | 0 | 2 | 700 | 100 | - | 450 |
| Red hartebeest | 4 | 5 | 5 | 14 | 4 | 6 | 4 | 14 | 0 | -17 | 25 | 0 |
| Springbuck | 0 | 2 | 1 | 3 | 2 | 3 | 2 | 7 | -100 | -33 | -50 | -57 |
| Springbuck (black) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | - | 0 | 0 | - |
| Warthog | 2 | 15 | 5 | 22 | 1 | 2 | 3 | 7 | 100 | 650 | 67 | 214 |
| Waterbuck | 1 | 0 | 3 | 4 | 3 | 4 | 3 | 9 | -67 | -100 | 0 | -56 |
| Wildebeest (black) | 17 | 4 | 4 | 25 | 3 | 6 | 3 | 13 | 467 | -33 | 33 | 92 |
| Wildebeest (blue) | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | - | - | 0 | - |
| Zebra | 2 | 3 | 0 | 5 | 5 | 6 | 6 | 17 | -60 | -50 | -100 | -71 |
| | | | | | | | | | | | | |
| Total kills | 89 | 94 | 44 | 227 | 102 | 138 | 110 | 375 | -13 | -32 | -60 | -39 |
| Days in subsample | 128.0 | 150.5 | 90.0 | 368.5 | | | | | | | | |
| No. of lions | 7.5 | 8.3 | 11.4 | 9.1 | | | | | | | | |

## DISCUSSION

The lions on Shamwari exhibited similar hunting behaviour to that which has been reported elsewhere. They selected a wide range of prey of all sizes, including non-mammalian species. However, as many studies have shown, the majority of the diet was made up of only a few species (Schaller 1972; Rudnai 1974; Mills 1990; Stander 1992; Packer *et al.* 1995). The majority of the lions' diet was made up of large species such as kudu (29.5%), wildebeest (11.7%), eland (5.3%) and red hartebeest (4.5%) which is consistent with previous studies (Funston *et al.* 1998; 2001).

In this study lions killed more male ungulates than female and previous research has shown that lions preferentially select males over females (Schaller 1972; Rudnai 1974; Mills 1990; Ruggiero 1991; Stander 1992a; Owen-Smith 1993; Viljoen 1997; Hunter 1998). At a proximate level, predation directly affects patterns of sex ratio variation among adult ungulates, although life-history traits predispose sexes to differential mortality and the extent to which predators may influence these ratios (Berger & Gompper 1999). For example, with species that form small bachelor groups or where the males are often solitary, as is the case in most polygynous mating systems, the males are more vulnerable because they do not have the benefit of increased vigilance through the 'many eyes' effect (Hunter 1998). When lions hunt small herds of 1-3 animals they have a higher probability of success than when hunting herds of more than four animals (van Orsdol 1984; Funston *et al.* 2001). Viljoen (1997) analysed seven studies and determined that lions kill a greater proportion of juveniles than would be expected from their relative numbers in the population. However, in the present study, more adult's kills were recorded than either juveniles or subadults. Since the relative contribution of each age class to the total ungulate population is unknown, it cannot be determined whether the lions are hunting adults selectively or at random. The sex and age classes of prey species selected by lions have important wildlife management implications, particularly as they can serve as a basis for the calculation of food consumption which in turn can be used to calculate estimated annual offtake. In addition, this information is essential if one is to attempt to model the effect of predation on ungulates. As discussed earlier, daily intake rates are most reliable when the age, sex and approximate amount of meat consumed off every carcass is known, as well as the number, age and sex of the lions which fed on each carcass. This was not possible in this study due to the opportunistic nature of the data collection, however it does highlight the type of information that should be collected for accurate analyses. An analysis of sex and age classes of animals killed by predators is also essential in gaining a greater understanding of the possible effects of predators on prey populations (Viljoen 1997).

According to Stander (1992) preference indices are an indication of the vulnerability of a species to its predator and are influenced by spatial distribution of the prey and hunting success of the predator when hunting that species. True preference for prey can only be determined through direct observation of selection when lions are presented with a choice of prey species (see Stander 1992). This was not possible during this study and the preference rating was assumed to reflect the selective preferences of the lions for each species.

The similarity in calculated prey preference indices between the full and subset of data is intriguing since it was assumed that the smaller prey species would have been under-represented in the full data set. It appears that this was not the case and both data sets equally reflect the prey preference of lions at Shamwari. The reliability of the two data sets will be dependant on their sample sizes. This is illustrated in year 3, where the decrease in number of kills observed resulted in proportionally fewer kills observed within five days of each other relative to years 1 and 2. The proportional decrease is reflected in the large differences in preference ratings between the full and subset of data for waterbuck, red hartebeest, eland, warthog, ostrich and black wildebeest.

Ostrich, warthog and wildebeest had the highest overall preference indices, suggesting that they were hunted more than would be expected if the lions were hunting according to abundance. However, high preference indices should be interpreted with caution since, while they may reflect true preference, they can easily be artificially elevated. For example, if the population of a prey species on a reserve is very small, then a single predation incident will produce a very high preference index. Similarly, if an important prey species is undercounted in the game count process, then this would generate an artificially high preference index. Ostrich were present in low numbers on the reserve, are a conspicuous species and were previously naive to predators. By contrast, the rating for warthog was probably exaggerated due to the game count method which may have underestimated the species. The high rating for wildebeest probably reflects a true preference, and there is a well-documented tendency of lions to select this species (see Appendix 2). For example, Berry (1981) found that wildebeest had a preference index of 2.98 in Etosha National Park. In the present study, kudu was the most important prey species in the lions' diet and the preference rating of close to one was a result of it being one of the most abundant species on the reserve. The species with the lowest preference indices on Shamwari were those that fall within the small size class. This could indicate a bias in the recording of kills because small prey items are more easily hidden and more rapidly consumed than larger items (Bertram 1979; Ruggiero 1991; Stander 1991). If this was the case, then the observed kills would be low and this would create a low preference index. To a certain extent this tendency to produce artificially low preference indices for the small prey species will be countered by the fact that many of the small species (common duiker, bushbuck) are difficult to count and the game counts will be low. It is important to note that, while carcass records may provide a biased view of lion diets because carcasses of larger prey are often over-represented, such records can be extremely useful for comparative purposes (Ruggiero 1991; Dunham 1992).

The daily intake rates for the subset of data were almost certainly more reliable than those calculated from the full data set because of the bias introduced in the latter by long periods during which kills were not recorded. Daily intake rates from both data sets decreased from year 1 to year 3. This may be a result of the lions changing their feeding habits over time, or the observations of kills becoming increasingly more inaccurate and unreliable. It is likely to be a combination of the two factors. The low value for the third year can be ascribed to the increase in FEQs as the cubs born in the first year reached the subadult feeding category, and a concurrent decrease in the observation effort, the number of observed kills and therefore estimated biomass consumed during the year. Since the kills observed only reflect the minimum number of kills actually made, it is evident from the subset of data that the lions' daily intake on Shamwari was higher than what has been observed elsewhere (see Appendix).

Lions at Shamwari killed more than was necessary to meet their energy intake requirements, assuming these requirements to be the average of observed intake (7.12kg/FEQ/day). This is illustrated by the high intake rate in year 1 and by incidences during the study period when larger ungulate species were only partially eaten or abandoned without being fed upon. For instance, in year 2 the southern females together with the pride male killed three adult eland and an adult female giraffe within a period of two days and none of the carcasses were completely consumed. This may be due to the fact that, when presented with a high density of prey, lions will kill more often than necessary (see Packer *et al.* 1990; Stander 1991). It is also the case that the ungulates had no prior experience of large carnivores and this may have made them easy prey for the lions in the first year. This has important consequences when reintroducing lions to these types of reserves. The artificial nature of small, closed reserves could bring about a change in the known behaviour of large predators as well as their prey as they adapt to their new situation. There is an urgent need for a better understanding of these dynamics if both predator and prey species are to be managed for optimal coexistence.

The total estimated removal per year more closely matched the results from the analysis of the subset of data than the full set of data for both intake rates although there was considerably more difference between year 3 and all four estimations of removal. For the subset, there was a strong similarity between the total kills for year 1 and the estimated offtake derived using 7.12kg/FEQ/day. Year 2 of the subset, on the other hand, was very similar to the estimate calculated using 5kg/FEQ/day. This appears to support the observation made earlier that the lions decreased their intake of food in the second year. The third year of observations did not yield results which were consistent with either calculation. This is largely due to a decrease in the number of kills observed during that year as a result of the removal of radio collars from male lions and the expiration of internal transmitters in the lionesses. The increase in the estimated removal from the first to the third year is to be expected since the number of lions increased over this time. The variation between the estimated and observed removals for some species suggests that there is some measure of preference for certain species. This is evidenced by the fact that the three species with the highest preference ratings (ostrich, warthog and black wildebeest) were also the species that had the greatest positive differences between observed and estimated offtakes (Table 3.13).

Table 3.13. Comparison of the preferences, size class and differences between observed and expected annual offake at daily intake rates of 5kg/FEQ/day and 7.12kg/FEQ/day for species killed by lions.

| Species | Preference | Size | Differences | |
|---|---|---|---|---|
| | | | 5 | 7.12 |
| Mountain reedbuck | 0.06 | Small | -83 | -89 |
| Impala | 0.09 | Small | -87 | -91 |
| Duiker | 0.24 | Small | -9 | -38 |
| Springbuck | 0.31 | Small | -40 | -57 |
| Bushbuck | 0.44 | Small | 13 | -25 |
| Zebra | 1.22 | Large | -58 | -71 |
| Blesbuck | 1.30 | Medium | 64 | 13 |
| Waterbuck | 1.33 | Large | -33 | -56 |
| Gemsbok | 1.46 | Large | -43 | -64 |
| Kudu | 1.87 | Large | -26 | -50 |
| Red hartebeest | 2.20 | Medium | 40 | 0 |
| Eland | 2.29 | Large | -31 | -72 |
| Giraffe | 2.42 | Large | -75 | -82 |
| Warthog | 4.35 | Medium | 450 | 450 |
| Wildebeest | 5.49 | Large | 178 | 92 |
| Ostrich | 6.78 | Medium | 450 | 450 |

At the other end of the prey preference scale, impala and mountain reedbuck, which had the lowest prey preference indices also had the greatest negative differences between observed and expected values. The high negative differences indicate that the lions are killing fewer than expected if predation is at random and this supports the very low preference index. Alternatively, the same results would be generated if large numbers of reedbuck and impala kills were missed by opportunistic observation. While this may be the case for mountain reedbuck because of the terrain they inhabit, it is unlikely to be the sole explanation for impala which is a plains and savanna species and kills are, therefore, more easily detected. The most obvious anomaly is the giraffe which has a high preference index but for which the observed kill rate is lower than predicted. While the prey preference index and the difference between observed and expected predation rates are both measures of preference, the prey preference index is calculated at a whole animal level and the other is calculated on a biomass basis. Thus giraffe, which are present in small numbers but are large and make a substantial contribution to the total biomass will perform differently in the two analyses. It is important to note that the accuracy of the preference index and the estimated offtake is reliant on the accuracy of the kill list and the population census, and that errors in either will create biases. It may be possible to overcome this problem by comparing the results from a range of different census methods but population censuses are costly and time-consuming and most reserves have a standard procedure that they follow in order to make comparisons between years more reliable.

Post-release studies are important when reintroducing animals because they not only provide a better understanding of the reaction of animals to a change in environment and hence allow better management in the future, but also provide baseline data from which management can monitor the changes in behaviour of the prey and predators and the effects of predators on their prey. The feeding biology of the Shamwari population of lions is likely to continue to change over time with increasing population size, changing prey availability (Dunham 1992; Fuller & Sievert 2001) and the intervention of active population management which is likely to disrupt established social systems. By monitoring populations of lions in small reserves it will be possible to gain insight into the effects of these management practices. Long term studies are important in determining the effects of management practices as well as the effects of extended dry and wet periods on both the lions and their prey population. Previous studies have shown that dry periods can exacerbate the effects of predation on a species (Pienaar 1969; Berry 1981; Mills *et al.* 1995; Harrington *et al.* 1999; Ogutu & Owen-Smith 2003).

While there may be biases in the method of observing kills, it must also be accepted that few reserves of small size will employ a person(s) to observe the lions full-time for extended periods of time. Data are most likely to be based on opportunistic sightings by rangers or guests. This study shows that using a subset of data improves the reliability of results in terms of daily food intake and makes comparisons of observed and expected intake more consistent. However, in this study, analysis of the subset of data did not affect the relative proportions of age and sex classes or preference ratings of prey. With this in mind, it is necessary to collect accurate records on age and sex and proportion of the carcass consumed as well as the age, sex and number of lions present at the kill. Goodman's formula, which calculates offtake of species according to relative biomass on the reserve, could be used to calculate the total annual offtake if the sample size is robust enough and reliable intake rates are used (either from the literature or from a long term study of the population). Bearing in mind anomalies such as giraffe, the formula can also highlight the species which are being preferentially selected by lions, in much the same way as Pienaar's (1969) preference index, so that these populations can then be more carefully monitored.

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# CHAPTER 4

## Analysis of body condition of animals killed by lions and evaluation of the bone marrow analysis technique

### INTRODUCTION

The physical condition of an animal has been suggested as a sensitive and easily measured response to the condition of its habitat (Riney 1982). Body condition indices have been used to assess habitat quality and resource use (Attwell & Bhika 1984; Stelfox & Hudson 1986; Shackleton & Granger 1989) as well as the effects of current or past management practices, stocking rates, weather and other ecological conditions (Smith 1970) on animal condition. In predator-prey studies, the physical condition of prey selected by predators has important implications, particularly when the condition of the prey population is known (Davis *et al.* 1987; Takatsuki 2000). When ungulates are free from predation, their populations often increase to close to the carrying capacity of their habitats (Takatsuki 2000). Under these conditions the nutritional status of the populations becomes poor and can result in a reduction in body size, a decrease in reproductive output or an increase in mortality, particularly in young and old animals (Takatsuki 2000). For example, Anderson (1985) found that for nyala populations under nutritional stress there are significant biases in the age distribution of adult mortality, and fewer young adults and more old adults die than would normally be expected. Animals in poor condition are more susceptible to predation (Hirst 1969, Temple 1987). Sinclair & Arcese (1995) reported that populations of wildebeest that were exposed to predation were in better condition than populations that were free from predation. This supports the "predator regulation" hypothesis that predators hold prey populations well below starvation levels and consequently individuals are in good condition. Not all researchers agree however, and for example Pierce *et al.* (2000) found that neither mountain lions nor coyotes selected individuals that were malnourished. If lions select young, healthy individuals over old, malnourished or diseased animals from a prey population that contains animals in both good and poor condition, there are important consequences for management. Healthy, reproductively active individuals are necessary to sustain a prey population but if the lions are targeting these animals, then the number of individuals of a species killed by lions is not as important as the selection of those individuals. Monitoring the condition of animals killed by lions will provide a more accurate estimation of the impact of lions on their prey species within a reserve.

According to Smith (1970), a method of condition determination should be as quantitative and objective as possible and the data should be easy to collect. The method should enable different investigators to obtain data with comparable accuracy in order to validate comparisons of populations from different areas and at different times (Smith 1970).

Fat deposits have been used as indicators of nutritional status of domestic animals since the beginning of the 1900s, but it was only after the 1950s that these deposits were used for wild animals (Takatsuki 2000). The most commonly used indicators have been visual body condition score (VBS); kidney fat index (KFI); and marrow fat index (MFI). All three have their own advantages and disadvantages.

The VBS has been used extensively by researchers (Riney 1955) and game managers. The advantage of this method is that it can be used to assess the nutritional status of live animals. The disadvantages are that, as a subjective evaluation of an animal's condition, is not precise and not easily repeatable.

In general, kidney fat has been found to be the most reliable indicator in many ungulates (red deer, Riney 1955; Batcheler & Clarke 1970; Mitchell *et al.* 1976; Himalayan thar, Caughley 1970; mule deer, Anderson *et al.* 1972; barren-ground caribou, Allaye Chan-McLeod *et al.* 1995). The KFI is simply the ratio between the weight of the fat tissue around the kidney and the weight of the kidney, which makes it a rapid and relatively objective quantitative measure of fat deposition. This method has subsequently been used by other authors (notably Hughes & Mall 1958; Taber *et al.* 1959; Ransom 1965; Sinclair & Duncan 1972; Attwell & Bhika 1984; Anderson 1985; Allaye Chan-McLeod *et al.* 1995). However, Takatsuki (2000) suggests that the kidney fat index is a good indicator of nutritional status for deer in good condition, but not a good indicator of individuals in poor condition because at low KFI values the KFI becomes less 'sensitive' to differences in MFI values. In other words, the relationship is between KFI and body condition is not linear. This may be a disadvantage, depending on the type of information that is required. A further disadvantage is that the kidneys, along with their fat deposits are often eaten by predators or deteriorate rapidly when exposed to the environment, and thus the KFI may not be a suitable technique for analyzing the condition of carcasses.

The fat content of bone marrow has also been widely used as a means of assessing the condition of ungulates (for example Cheatum 1949; Ransom 1965; Sinclair & Duncan 1972; Brooks *et al.* 1977; Mech & DelGiudice 1985; Ballard & Whitman 1987; Pierce *et al.* 2000) and birds (Thouzeau *et al.* 1997; Baduini *et al.* 2001). As an animal's nutritional status declines, the fat stores are used in the following order: subcutaneous, omental, renal, pericardial, and finally marrow (Sinclair & Duncan 1972; Brooks *et al.* 1977). Thus the fat reserves in bone marrow are only mobilised after most of the perinephric fat has been utilized (Bear 1971; Brooks *et al.* 1977; Anderson 1985; Sinclair & Arcese 1995). This means that if the marrow has lost any fat, the individual is probably in poor condition. However, an individual may have lost most of its total body fat yet still retain a high percentage of marrow fat. Such an animal cannot be considered to be in good condition, illustrating the pitfalls of the bone marrow fat analysis (Mech & Delguidice 1985). In general, bone marrow is more easily and more reliably collected than subcutaneous fat, especially from animals killed by predators. In these instances, analysis of marrow fat may be the only method of determining the condition of the prey animal and for this reason, bone marrow was selected as the method for determining condition of animals killed by lions in the present study.

Marrow consists of three basic components: water, fat and non-fat residue of which the latter consists of cell membranes, blood vessels and a small amount of blood (Williams *et al.* 1989). Marrow fat has been estimated in a number of ways, including: chemical extractions (Neiland 1970), visual estimation (Harris 1945; Cheatum 1949); compression (Greer 1968); oven drying (Neiland 1970); reagent-dry assaying (Verme & Holland 1973); and freeze drying (Hunt 1979).

Chemical methods of fat estimation measure all three components but are expensive, time-consuming and tedious (Sinclair & Duncan 1972). The several drying techniques are relatively fast, inexpensive and sufficiently accurate for most studies (Hunt 1979). However, they measure only water and fat and make the assumption that the contribution that the non-fat residue makes to the bone marrow is negligible and constant. Neiland (1970) found that there was a good relationship between the dry weight of the bone marrow as a percentage of its fresh weight, and the fat content as a percentage of the fresh weight. However, he also stated that subtracting the average residue value produced more accurate results. Other researchers have recommended that a regression be used to correct for non-fat residue. Sinclair & Duncan (1972) suggest the formula:

$$\% \text{ fat} = \% \text{ dry weight} - 6.$$

The constant (6) represents the non-fat residue in the fat after drying and is approximately the mean of the residues obtained from blue wildebeest (7.2829), Coke's hartebeest (6.9483) and buffalo (3.4182). Brooks *et al.* (1977) showed that for eight African ungulates this regression constant varied from 5.04 to 10.33 with a mean of 7.12 and suggested that for the purposes of condition assessment, a value of 7 should be used to produce an acceptable and easy to use relationship.

Researchers have found that, on the occasions when marrow was sampled from bones other than femurs, there was some variation in the fat content of the various bones (Peterson *et al.* 1982; Fuller *et al.* 1986; Davis *et al.* 1987). It was found that fat depletion generally advances more rapidly in proximal bones, such as femurs and humeri, than distal ones, such as radii and tibia, but that correlations were high in all regressions between the bones (Brooks *et al.* 1977; Peterson *et al.* 1982; Fuller *et al.* 1986; Davis *et al.* 1987). This is a useful finding because it allows an estimate of condition to be made from bones other than the femurs, which are often carried away by predators and scavengers (Sinclair & Duncan 1972; Davis *et al.* 1987). Davis *et al.* (1987) concluded that, while bones other than femurs may be valid indicators of relative condition, it is necessary to regress marrow values for all long bones and mandibles to the femur standard, and that this standard may differ between species.

Due to the variable nature in the responses of animals to resource shortage, it is difficult to predict at what percentage bone marrow fat an animal will suffer reproductively or physiologically or when death is inevitable. Brooks (1978) assigned the term 'good' to the level of condition prior to the mobilization of marrow fat (MFI > 85%). Bone marrow is not mobilized until most of the kidney fat has been utilized (Sinclair & Duncan 1972) or when KFI drops below 40, above which the mean MFI remains above 85% (Brooks *et al.* 1977; Brooks 1978; Takatsuki 2000). Below this level an arbitrary division into moderate (MFI 50% - 85%) and poor condition (<50%) must be made due to the lack of knowledge discussed above (Takatsuki 2000).

This study aims to determine the condition of animals killed by lions and, in an attempt to refine the current methodology, whether the fat content of bone marrow can be accurately determined from dry weight, whether distal bones can be used for body condition analysis, and whether bones that had been collected one week after an animal was killed were still useful for analysis.

## METHODS

### *Marrow samples*

Intact bones were collected from various sources for each analysis. When testing the accuracy of determining the fat content of bone marrow from dry weight, bones were used from animals killed by lions and cheetah and from those culled for population control purposes. This was done to ensure a wide representation of values for regression analysis. Only animals killed by predators were used for the comparison of dry weight between proximal and distal bones, since only proximal bones were available from culls. The experiment involving exposure of bones to the environment was carried out using bones from culled animals only because they could be collected and frozen within a few hours of the animal's death. All animals came from Kwandwe between March and October 2003. Only bones from sub-adult (>2 years old) and adult (reproductive) animals were analysed due to the highly variable and age-dependant nature of juvenile fat stores (Ballard & Whitman 1987; Adams 2003). Bones from predator kills were collected as soon as the predators had moved out of the area where the kill had been made. All samples were frozen in plastic bags with a label indicating the species, bone, the date the kill was made, the date the bone was collected, the predator responsible for the kill and the location with GPS coordinates. Bones from culled animals were kept in cold storage and frozen within 24 hours of collection. Bones remained frozen until analysis (Neiland 1970; Anderson 1985; Fuller *et al.* 1986; Davis *et al.* 1987; Takatsuki 2000), which was sometimes several weeks after collection.

### *Calculation of dry weight of marrow*

For this analysis, a portion of bone marrow was removed from the central area of the bone, avoiding the hemopoietic end regions (Neiland 1970; Brooks *et al.* 1977, Davis *et al.* 1987, Takatsuki 2000). The sample was secured by cracking the middle of the bone with a hammer and chisel. Wherever possible, samples of 5-15g, measured to the nearest 0.01g, were used. The samples were then placed in crucibles and oven-dried at 60-70°C. Each sample was reweighed on a daily basis until there was no change in the weight. As Davis *et al.* (1987) also found, this usually took 3-6 days.

The average condition of animals killed by lions (n = 25) and those culled from the population (n = 48) was calculated from oven-dried samples. The samples were then further analysed in terms of species (kills and culls) and sex (kills only) in order to determine whether either factor affected the average dry weight of the marrow.

### *Calculation of non-fat residue of marrow*

To determine the relative contribution of non-fat residue to the dry weight of marrow, oven-dried samples from both lion and cheetah kills and culled animals were then run through a Soxhlet extractor for 12 hours using chloroform to separate the fat from the non-fat residue (adapted from Neiland 1970). The percentage dry weight was compared with the relative fat (mass of fat as a percentage of the mass of the wet marrow) for all species combined (n =45) as well as for impala (n = 27), which was the only species for which the sample size was suitable for independent analysis. The resulting regressions were compared with the corresponding equations proposed by Brooks *et al.* (1977) by substituting the dry weights of marrow in the bones before fat extraction, into their equation. The two regressions were tested for statistically significant differences using paired t-tests (Statistica 6).

### *Proximal and distal bones*

The relationship between the % dry weights of marrow from proximal and distal bones were compared by analyzing combinations of femurs and tibias/fibulas and humeri and radii/ulnas from the same legs of animals killed by lion and cheetah (n = 20). Dry weight of marrow from related bones was analysed statistically using paired t-tests (Statistica 6).

### *Effects of exposure*

The hypothesis that prolonged exposure to the environment would cause water loss from bone marrow and therefore give a misleadingly high MFI was tested in order to establish the reliability of MFI values from bones not collected within 24 hours of a kill being made. Bones from culled animals (n = 48) were divided into two groups, control (n = 24) and experimental (n = 24). All bones were initially frozen and bone marrow was extracted from the control group immediately after defrosting. The experimental group of bones was hung out exposed to the elements for a period of one week before bone marrow was extracted. Since water is the first component to evaporate, it is expected that as bone marrow deteriorates, the percentage dry weight should increase. Dry weights were analysed statistically using t-tests (Statistica 6). This experiment was only carried out in the winter months and seasonal variation in deterioration rates was not examined.

Statistical analyses were limited to t-tests throughout due to the small, often unequal samples or unbalanced design. This was due to the unavoidably opportunistic nature of the bone collection.

## RESULTS

### *Calculation of dry weight*

The overall condition (or MFI) of animals killed by lions was moderate to good with an average marrow dry weight of 76.6% (Table 4.1) although the average condition of gemsbok and kudu was lower. This can possibly be explained by the fact that all gemsbok and nine out of ten of the kudu bones sampled were from adult bulls and, as is seen in Table 4.2, condition was significantly lower for males than females ($p < 0.05$). The overall condition of culled animals was much lower than that of kills with a mean marrow dry weight of 59.7% (Table 4.3). However, this should be interpreted with care since it was the impala that were in poor condition and they comprised forty-one of the forty-eight specimens (Table 4.3).

Table 4.1. Condition of lion kills analysed in terms of prey species with sample sizes and mean and standard deviations of % dry weight of marrow for each species.

| Species | n | Mean and sd of % dry weight |
|---|---|---|
| Eland | 7 | 87.1±15.7 |
| Gemsbok | 3 | 54.6±25.6 |
| Kudu | 10 | 69.2±27.8 |
| Waterbuck | 1 | 93.6 |
| Wildebeest | 2 | 91.6±1.2 |
| Zebra | 2 | 86.3±7.2 |
| Total | 25 | 76.6±23.7 |

Table 4.2. Comparison of the condition of male and female animals killed by lions with sample sizes and mean and standard deviations of % dry weight for each sex.

| Sex | n | Mean and sd of % dry weight |
|---|---|---|
| Female | 11 | 87.8±12.7 |
| Male | 12 | 64.8±27.9 |
| Unknown | 2 | 86.3±7.2 |
| Total | 25 | 76.6±23.7 |

Table 4.3. Condition of culled animals analysed in terms of prey species with sample sizes and mean and standard deviations of % dry weight of marrow for each species.

| Species | n | Mean and sd of % dry weight |
|---|---|---|
| Impala | 41 | 56.2±25.4 |
| Kudu | 1 | 88.5 |
| Springbok | 1 | 91.5 |
| Warthog | 5 | 76.2±35.0 |
| Total | 48 | 59.7±27.1 |

*Calculation of non-fat residue*

Forty-five bones from nine species (including lion and cheetah kills and culls) were further analysed using Soxhlet extractions. When bones from all species were combined the regression between dry weight and fat as a percentage of the original weight of marrow was $y = 1.2355x - 25.96$ ($r = 0.9763$; $n = 45$). This regression was significantly different ($p < 0.0001$) from the equation proposed by Brooks *et al.* (1977) of $y = x - 7$ (Figure 4.1). The regression equation for impala was $y = 1.2286x - 26.436$ ($r = 0.9691$; $n = 27$) which was significantly different ($p < 0.0001$) from the equation proposed by Brooks *et al.* (1977) for impala of $y = 1.03x - 7.14$ (Figure 4.2). A possible explanation for the clustering of points at low fat values is that the culling period fell within the post-rut season when male impala have lower than normal body condition (Brooks 1978).

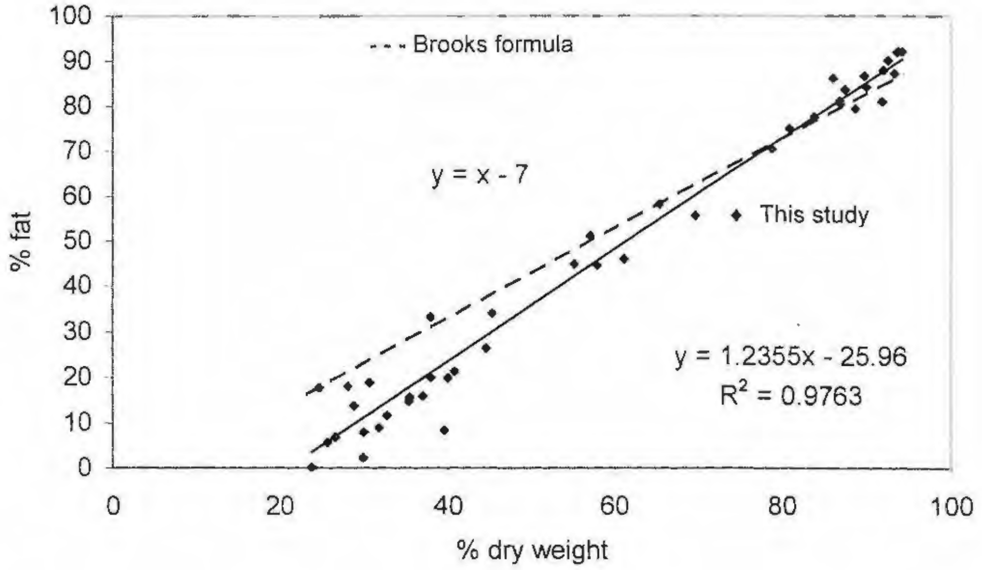

Figure 4.1. Relationship between % marrow fat calculated after Soxhlet extraction and % dry weight of marrow for African ungulates as determined by this study and by Brooks *et al.* (1977).

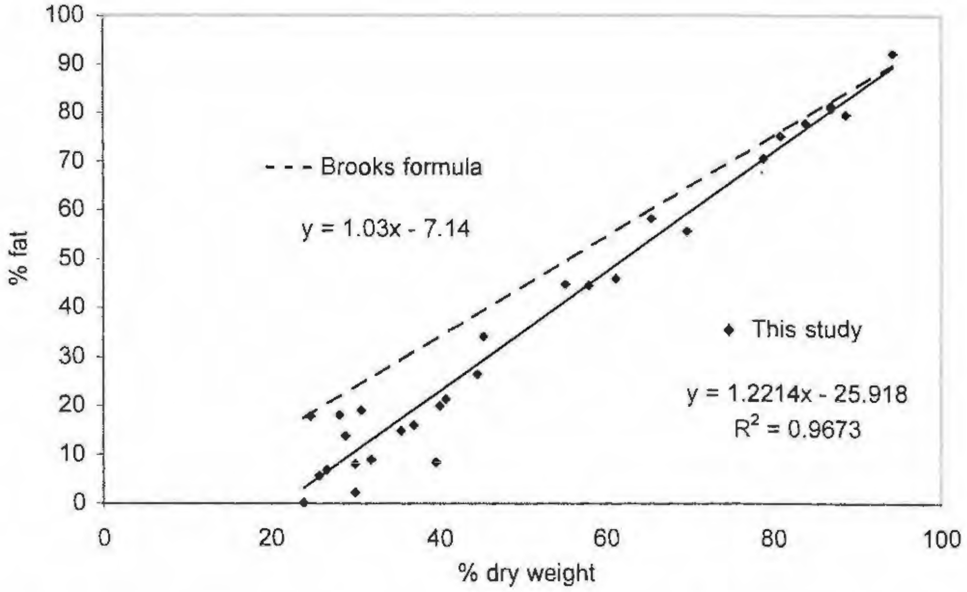

Figure 4.2. Relationship between % marrow fat calculated after Soxhlet extraction and % dry weight of marrow for impala as determined by this study and by Brooks *et al.* (1977).

*Proximal and distal bones*

The relationship between the dry weight of marrow from distal and proximal bones (Figure 4.3) can be expressed by the equation $y = 0.8834x - 1.1549$ ($r^2 = 0.812$; $n = 20$ pairs). This indicates that there is only a slight difference between dry weight values for distal and proximal bones, although values for distal bones should be adjusted using the above regression so that they can be compared to a proximal bone standard. Figure 4.3 shows that thirteen pairs of bones had high MFI (>80%) for the distal bones but there was substantial variation in the MFI for the corresponding proximal bones (30 to 95%). There was less deviation from the regression line at low marrow fat values.

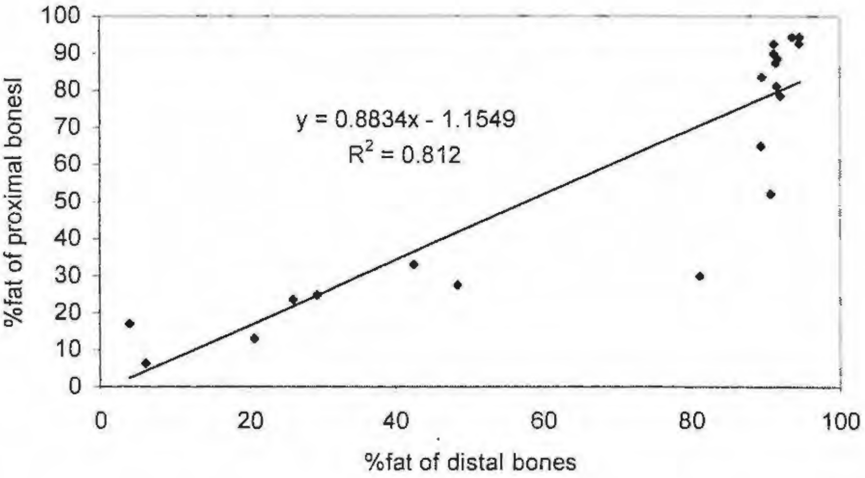

Figure 4.3. Regression between percentage dry weight of marrow from proximal and distal bones (n=16 pairs).

*Effects of exposure*

The hypothesis that exposure of bones to the environment would result in an increase in the MFI was not supported by the results and there was no significant effect of exposure of bones to the elements on MFI (Figure 4.4; $p > 0.05$). The mean and standard deviations for the control and experimental were almost identical and there was no biologically or statistically significant difference between the two ($p = 0.443145$). The relatively low mean values for all bones can be attributed to the high proportion of impala males in the samples.

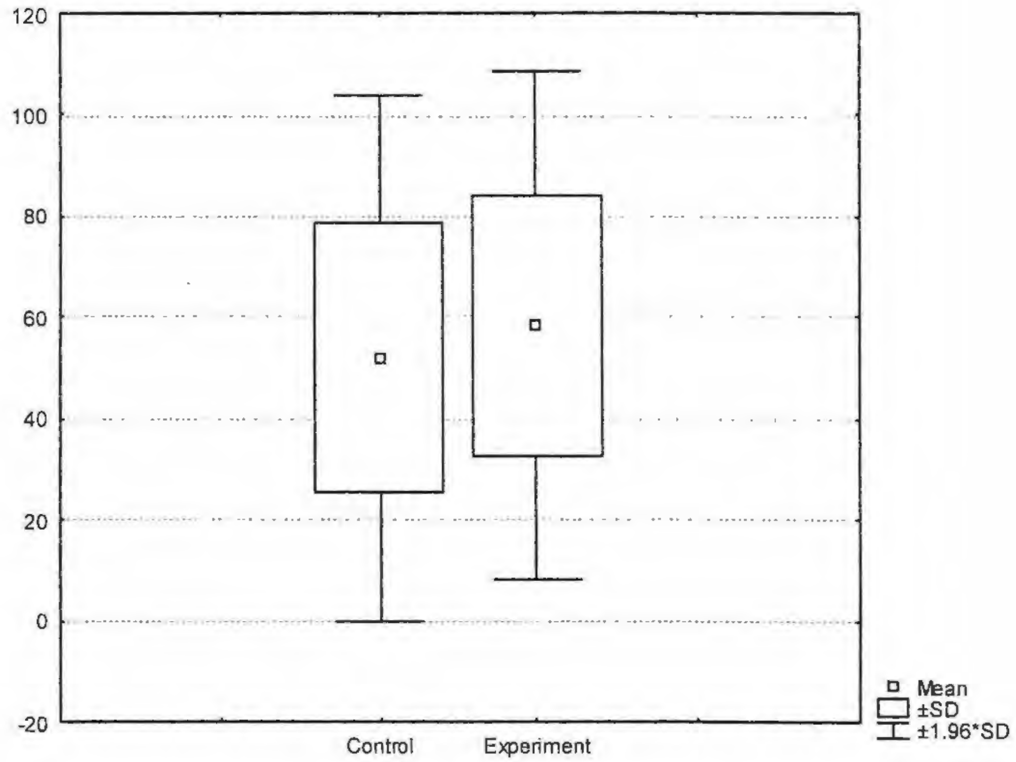

Figure 4.4. Relationship between % dry weight of marrow from bones analysed immediately upon defrosting (control) and bones that had been exposed to the elements for a period of one week (experiment).

## DISCUSSION

Due to the opportunistic collection of bones from kills and culled animals, it was not possible to collect equal samples of specimens representing all species and sexes, but from the material available certain relevant and significant trends emerge.

Animals killed by lions in Kwandwe were in moderate to good condition and, while the small sample size does not allow statistical examination of interspecific variation, there are trends that warrant further investigation and these are discussed below. Sinclair & Arcese (1995) and Mduma *et al.* (1999), using visual bone marrow estimation to determine body condition, found that Serengeti wildebeest that were killed by lions were in moderate to good condition but that their condition was significantly poorer than samples culled randomly from the live population. Sinclair & Arcese (1995) concluded that both food and predation limit populations because as food becomes limiting, animals take greater risk to obtain more food making them more vulnerable to predators. Animals killed in this way will not necessarily be in poor condition because they may not yet have reached starvation levels but they are likely to be in poorer condition than the rest of the population (Sinclair & Arcese 1995).

Conditions of female and male wildebeest killed by lions were similar in the study by Sinclair & Arcese (1995) but in the present study females were in good condition while males were in moderate condition. Since nine out of the twelve male specimens examined were kudu, these data should be interpreted with caution since what appears to be a gender-related effect may be limited to male kudu only. Factors such as nutrition, genetics, pathology, climate and reproduction, which all influence condition (Smith 1970; Anderson 1985), may be responsible for the differences between the sexes. Female nyala (Anderson 1985), wapiti (Flook 1970 in Anderson 1985) and pronghorn antelope (Bear 1971) have significantly higher KFI levels than males which may be because males attain a greater body size and therefore have greater requirements for growth and maintenance. Owen-Smith (1993) proposed that, apart from being less agile, male kudu are more susceptible to predation due to malnutrition brought about by increased food demand and resultant increased tooth wear. The mating system of a species and the season will affect body condition (see discussion below for impala) however, the breeding behaviour of male kudu is of low intensity and the mating season does not affect their body fat reserves (Owen-Smith 1993). Interpretation of the results is problematic without comprehensive comparative data for the ungulates on the reserve and future research will address this. Larger sample sizes for a range of species from kills and culls will make interpretation of the data easier.

The low MFI for culled animals compared to that of kills suggests that lions were selecting for healthy individuals. However, the results of the culls are skewed by the impala marrow samples that formed the majority of the data set. The fact that the majority of impala were males culled shortly after the rut when their fat stores would have been low, highlights the importance of considering mating systems and season when determining the overall condition of a population.

A strong relationship was found between percentage dry weight and percentage fat content of bone marrow, which means that fat content can be estimated from dry weight. This is a useful finding because the oven-drying methods are simpler, cheaper and less time consuming than the chemical methods. Despite the significant differences between the equation proposed by Brooks *et al.* (1977) and the one derived from this study, there appears to be no biologically significant difference because the lines only diverge at low dry weights and the difference in percentage fat is less than 15%. Although the threshold below which an animal is unlikely to recover has not been determined, animals in very poor condition are unlikely to regain complete health and reproductive fitness. At high dry weights the two lines converge and there is almost no difference between the two equations. The statistically significant difference between the two regressions may be due to differences in the species analysed, habitat types or even the method of extraction used. Sinclair & Duncan (1972) ran the Soxhlet extractions for four hours and Brooks *et al.* (1977) ran them for eight hours with no significant difference between results. Therefore, the duration of extraction does not appear to influence the results. Brooks *et al.* (1977) used bone marrow samples from proximal and distal bones, which included metacarpals and metatarsals. Studies have shown that there are differences in dry weight between proximal and distal bones from the same animal (Peterson *et al.* 1982; Anderson 1985; Fuller *et al.* 1986; Davis *et al.* 1987), but especially between metacarpals or metatarsals and their related proximal bones (Fuller *et al.* 1986). The difference between metacarpals or metatarsals and their related proximal bones is in fact highlighted by Brooks *et al.* (1977), but the authors failed to accommodate this or reassess their regression calculation accordingly. Sinclair & Duncan (1972) found that there was very little difference between species in terms of non-fat residue and that a common regression could be applied. For this reason, and because the calculation of Brooks *et al.* (1977) may not be accurate, it is recommended that for estimations of body condition from the dry weight of marrow, the equation $y = 1.24x - 26$ be considered to correct for non-fat residue.

There was a strong correlation between the dry weights of proximal and distal bones, which suggests that whenever the femurs and humeri are not available or have been destroyed, the distal bones can be used as a suitable substitute after correction.

Fuller *et al.* (1986) found that the values for humerus marrow fat were nearly identical to corresponding femur levels but that the relationships between femur values and those for tibia and radius were more variable. Sinclair & Duncan (1972) found that the fat content of other bones did not differ by more than 10% from the fat content of the femur. In the present study, in a few cases where distal marrow dry weight was high, there was considerable variation (≈40%) between marrow dry weight for distal and proximal bones. In view of this, and the reported variation discussed above, dry weight of distal bones should be corrected to allow comparison. The variation in MFI for corresponding proximal and distal bones indicates that the fat from proximal and distal bones might be mobilized at differing rates from the two bone types. From the figure it appears that when the MFI for proximal bones is high, the MFI for distal bones is also high but that proximal bones lose fat more quickly than distal bones when the fat content drops below approximately 60%. It is at this stage that the marrow fat from distal bone appears to be mobilized. When more data are available, a non-linear relationship may be a more appropriate form of analysis and a different correction factor would need to be applied. However, given the strong correlation between the two bone types and the fact that the point of interest is whether or not the animal is in poor or good condition rather than a precise MFI value, it is suggested that the regression equation be used to estimate body condition from distal bones.

The slight difference found between the percentage dry weight of marrow from bones that were analysed immediately after defrosting and those that had been hung exposed to the elements means that carcasses which have been left in the open for up to a week can still be used to determine body condition. This is an important finding because predators often remain at a kill site until all the edible meat has been consumed and in some cases they may not move out of an area for several days. There may be seasonal variation in the rates of deterioration of bone marrow and although this has not been examined for logistical reasons it does require further research.

Body condition of prey should form an important part of predator-prey studies and it is demonstrated here that the dry weight of bone marrow is easily assessed and can be used to predict the fat content of marrow. Furthermore, because of the slow rate of deterioration observed, it can be used in predator studies where the bones are not immediately available for analysis. The opportunistic nature of the collection of bones in this study resulted in small and unbalanced sample sizes that made analysis of the results difficult. Future research should increase these samples making more detailed statistical analyses possible and producing more reliable relationships between values for proximal and distal bones and a better understanding of the effects of factors such as seasonality and sex on MFI.

The present study will provide the reserve with baseline data on the condition of animals killed by lions. Continued monitoring is a simple process and one that will provide insight into the response of the lions to changes in overall condition of the prey populations, particularly in times of drought. The condition of prey populations is easily monitored using MFI and this will highlight potential management problems such as the overstocking of herbivores. If the lion population is allowed to grow, the increase in the population's daily food requirements could mean that more animals in good condition are killed, especially if the size of hunting groups increases, and this will have a negative impact on the prey populations. However, it is important to know the body condition of the population of each prey species in order to determine whether there is selection or preference for animals in a particular condition by lions.

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# CHAPTER 5

# Characteristics of home range, habitat selection and habitat use by lions in Shamwari and Kwandwe

## INTRODUCTION

Lions display a greater degree of social interaction than most other felids (Schaller 1972; Hunter 1998; Funston *et al.* 2001) and live in fission-fusion social units, which allow them to forage as a group and to defend their young and their territories[1], more effectively (Gittleman 1989; Packer *et al.* 1990; Funston *et al.* 2001). Prides are stable social groups of related females together with their offspring and attendant males. Prides may occupy the same home range for generations and generally exclude unrelated females (van Orsdol *et al.* 1985; Hanby *et al.* 1995; Hunter 1998) although overlap between home ranges may occur. However, members of a pride do not necessarily all move together within the home range but may regularly split up and reunite (van Orsdol *et al.* 1985). The size of female home ranges is generally determined by density and distribution of prey, and will also be affected by the availability and spacing of suitable den sites for rearing cubs (Sunquist & Sunquist 1989; Hunter 1998). Males leave the pride as they approach sexual maturity and become nomadic unless they gain access to females by finding a pride that has lost its males, or by aggressively displacing the resident males (Elliot & McTaggart Cowan 1978; van Orsdol *et al.* 1985). Non-territorial males may remain solitary or form coalitions. The latter have competitive advantage over single males when competing for prides or territories. Bygott *et al.* (1979) found that in 19 out of 21 cases, coalitions of male lions were formed between relatives and that although single unrelated males can sometimes form stable pairs, they are often unable to form or join larger groups with unrelated males. Male home ranges are usually larger and

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[1] Home range is defined as the area a lion or pride occupies and defends against unrelated lions or non-pride members. It is used interchangeably with territory in this text. The terms core area and centre of activity are also used interchangeably and indicate the areas that are most often occupied (50% of the time)

may overlap a number of female home ranges to increase mating opportunities, and males will attempt to defend these territories from other males (van Orsdol *et al.* 1985; Hanby *et al.* 1995). It is clear that lions display complex patterns of social interaction and territoriality, which have important implications in their use of habitat (see Hunter 1998).

Considerable variation in home range size has been reported for lions (Macdonald 1983; see Appendix C). From data extracted from ten studies, van Orsdol *et al.* (1985) found that large home ranges overlap extensively with those of adjacent prides, while small home ranges tend to have little overlap. Van Orsdol *et al.* (1985) also found that, for thirteen studies of lions, home range size was inversely correlated with lean season biomass of prey species, which suggests that the minimum range size is determined by the food density during regular (or seasonal) periods of food shortage. The authors found no correlation between range size and group size which contradicts the findings of other researchers (Gittleman & Harvey 1983; Macdonald 1983) but they proposed an inverse relationship between range size and the number and size of prides in surrounding areas (van Orsdol *et al.* 1985). This has not been thoroughly investigated and, therefore, a long-term study on the change in home range size with increased number of lions, and the resultant increase in number and size of prides, within a small, closed reserve would be valuable.

Home range can be calculated in a variety of ways (see Dixon & Chapman 1980) but only two of the most commonly used methods will be discussed here. Comparisons of home-range size between studies should be made cautiously because the choice of software program, home-range estimators and input values of required parameters will influence the results (see Gallerani Lawson & Rodgers 1997).

The minimum convex polygon (MCP) method is the oldest method and has been widely used in home range studies (Boydston *et al.* 2003; Broomhall *et al.* 2003; Kamler *et al.* 2003; List & Macdonald 2003; Rodriguez-Robles 2003) including studies of lion home range (van Orsdol *et al.* 1985; Viljoen 1993; Stander 1997). It is often used to calculate home ranges so that the results are comparable with other studies. One of the disadvantages of this technique is that the area and shape are strongly influenced by outlying fixes (Harris *et al.* 1990; White & Garrott 1990; Powell 2000) and will include unused areas. The size of a home range calculated using the MCP method increases as the number of locations increases (see White & Garrott 1990) until it reaches an asymptote where additional locations do not add additional area.

Kernel-based estimates have recently become popular and have been used to study a variety of vertebrates (see Rodriguez-Robles 2003; List & Macdonald 2003) including large carnivores (Dixon & Chapman 1980; Hunter 1998; Boydston *et al.* 2003; Broomhall *et al.* 2003; Kamler *et al.*2003). The kernel density estimator, also called the utilization distribution (UD) method incorporates the density of known animal locations, giving more weight to frequently used areas, to produce a home range probability contour of any shape (Worton 1989; Powell 2000). This method uses a parameter, which is variously called the window width, bandwidth, smoothing parameter or *h*, to determine the level of detail in the output. When the window width is too small, fine structure becomes visible which obscures general trends in habitat use, while when it is too large the complex nature of an animals' home range may be obscured. Therefore, the process of examining several plots of data, with different values for window width, may give more insight into the data then merely considering a single automatically produced plot (Silverman 1986).

The number of observations needed to estimate home range size with MCPs has been suggested to be 29-150 for large carnivores (see Boydston *et al.* 2003), but kernel UDs do not require sample sizes as large as those required for MCPs (Powell 2000; Seaman *et al.* 1999). Where MCPs do not show intensity of use (Harris *et al.* 1990; Powell 2000), kernel UDs illustrate the relative amount of time an animal spends in a particular place (see Seaman & Powell 1996). Therefore, the kernel estimator together with least-squares cross-validation (LSCV), which determines window width, produces the most accurate estimates of home range areas and shapes of the density contour (Worton 1995; Seaman & Powell 1996; Seaman *et al.* 1998).

Very few data exist on the home range and habitat selection criteria of lions that are constrained by reserve size. In Queen Elizabeth and Nairobi National Parks and Ngorongoro Crater, physical barriers such as lakes, escarpments or human habitation may effectively restrict range expansion of prides if a decline in food availability occurs.

Consequently, it has been suggested that reserve size, configuration and topography are likely to influence the range sizes of some lion prides (van Orsdol *et al.* 1985).

This study aims to assess the selection and use of home ranges of lions in two small reserves in the Eastern Cape Province and, where possible, to compare this to lions in less restrictive circumstances. These data will serve as a base line against which future changes in space use and habitat selection can be compared.

## METHODS

### *Lion locations and kills*

GPS fixes of lion locations were recorded as often as possible by the reserve staff on both reserves using hand-held GPS units. On Shamwari, fixes were taken for kills only, while on Kwandwe an attempt was made to locate large predators by radio-telemetry or opportunistic sighting on a daily basis and kills were recorded whenever they were located. Data for Kwandwe lions were collected for each individual while data for Shamwari were collected for each pride or male lion. To avoid autocorrelation among sequential locations and to ensure that the data points were independent of each other, only one fix was used per day for each pride or animal (Gehrt & Fritzell 1998; Boydston *et al* 2003; Broomhall *et al.* 2003). Males and at least one member of each pride were fitted with radio collars and the remaining lions were fitted with internal radio transmitters.

### *Home range*

Home range sizes for lions on both reserves were calculated in Biotas$^{TM}$ 1.0.2 Beta using two non-parametric methods - the minimum convex polygon (MCP) method (White & Garrott 1990) and the fixed kernel utilization distribution (UD) method (Worton 1989; Powell 2000). The 50% and 95% home ranges were selected as they are generally considered to be the most robust estimators of an animal's centre of activity and of total home range size, respectively (Harris *et al.* 1990; White & Garrott 1990).

The MCP method was used to facilitate comparisons with previous studies and was calculated using the moving harmonic mean centroid.

The window width for the kernel-based estimates was initially calculated using LSCV for 50%, 75% (added for completeness) and 95% probability contours and then adjusted until it met the requirements for this study with regards to illustrating home ranges.

The location, shape and size of home ranges of Kwandwe lions were determined for the pride of two females (F1 and F2) and their cubs, the pride male (M1) and the solitary male (M2) as well as for each female individually, based on GPS fixes recorded between January and November 2003. On Shamwari, home range positions and sizes were determined for the two prides (Northern and Southern) separately using data collected between January and December 2002.

*Vegetation classification*

The vegetation maps for Shamwari (Figures 5.1) and Kwandwe (Figures 5.2) were created separately by the management of each reserve. They use different vegetation classification systems and different levels of detail and are therefore only comparable at a basic level. In the individual analyses of habitat use and selection for each reserve, the vegetation types (also called habitat types) were defined according to the available maps.

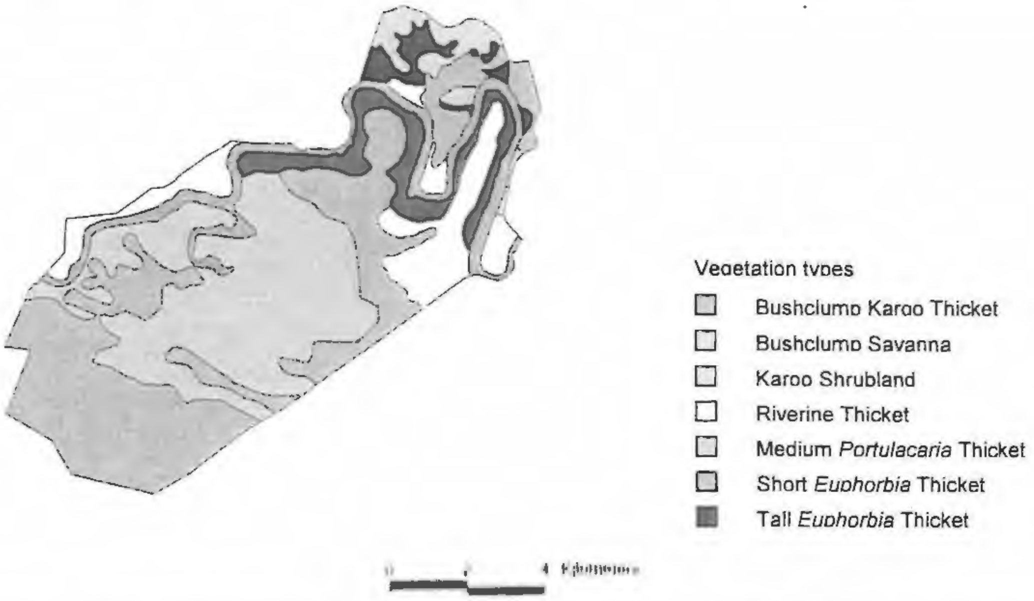

Figure 5.1. Map of Kwandwe Private Game Reserve showing the different vegetation types and their distribution in the reserve.

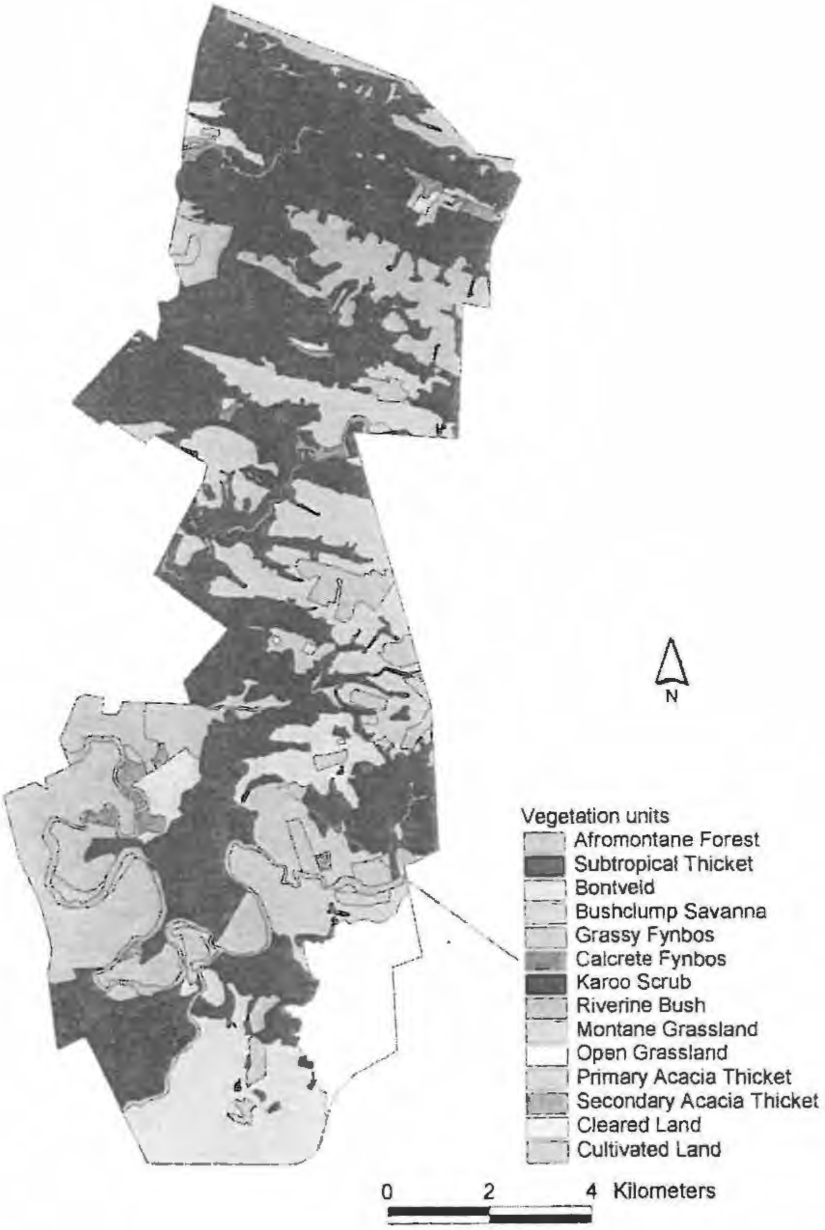

Figure 5.2. Map of Shamwari Private Game Reserve showing the different vegetation types and their distribution in the reserve.

*Habitat use and selection*

Habitat use is defined as the way in which an animal uses the physical and biological resources in a habitat (Krausman 1999). Habitat may be used for foraging, cover, denning or other life history processes. In this study, insufficient data meant that the different types of utilization could not be analysed separately and therefore 'use' refers to a lions' presence in a habitat type. Habitat selection can be defined as the "process of innate and learned behavioural decisions made by an animal about what habitat it would use at different scales of the environment" (Krausman 1999). The macrohabitat scale, which refers to landscape-scale features such as zones of specific vegetation associations, was used in the analysis. Analysis of habitat selection was performed at two levels for the 50% and 95% MCPs and UDs for each lion or pride. The first level is the proportion of observed utilization compared to the proportion of each habitat type available on the reserve. The second level is the proportional utilization of each habitat type within a lions' home range. The null hypothesis is that the lions are selecting habitat types, at both the reserve and home range level, according to the relative availability of each type, in other words habitat selection by lions is random. Technical problems with the Shamwari vegetation map prevented analysis of that reserve at the second level. Due to the nonstandard multivariate nature of the data, habitat selection within home ranges was investigated using compositional analysis (Aebischer *et al.* 1993), which tests selection of habitats by Wilk's lambda statistics in a multivariate analysis of variance (MANOVA). A habitat type that was available but not utilized by an animal was assigned a value less than the smallest recorded non-zero percentage (Aebischer *et al.* 1993), this value was calculated automatically by Biotas$^{TM}$. Statistical differences between use and availability were also calculated by Biotas$^{TM}$.

Preferential selection for each habitat type by each lion or pride at both levels of analysis was calculated as:

$$\text{Preference} = \frac{\text{proportional utilization}}{\text{proportional availability}}$$

The proportional utilization was calculated as the number of GPS fixes located in a habitat type as a proportion of the total number of fixes recorded for that individual or pride. The proportional availability was calculated as the area of a habitat type as a proportion of the total area available (either reserve size or home range size). Preference ratings greater than one indicate that the vegetation type was utilized more than expected according to its abundance, and a preference rating of less than one indicates that the vegetation type was underutilized with respect to its availability on the reserve. The number of vegetation types (i.e. sample size) was too small to calculate confidence intervals (see Chapter 3), therefore preference indices close to one were assumed to indicate random selection of that vegetation type.

## RESULTS

### *Home ranges and core areas*

For Kwandwe, M2 had the greatest 95% MCP (90.39km$^2$), which covered nearly two-thirds of the reserve (65.15%), while F1 had the smallest (42.93km$^2$), which covered just less than a third of the reserve (30.94%; Table 5.1). In comparison, M2 had the second smallest 95% UD (54.41km$^2$) of all home ranges while that of M1 was the largest (73.27km$^2$; Table 5.2). The 95% UD of F1 by the kernel method was comparable to her 95% MCP with an area of 49.82km$^2$ and covering 35.91% of the available space. The 95% UD of F1 was the smallest relative to the home ranges of the other lions.

The home ranges and centres of activity of the Northern and Southern Prides on Shamwari were smaller than those for lions in Kwandwe for both the MCP method (Table 5.3) and the kernel method (Table 5.4). The 95% MCP for the Northern Pride extended beyond the boundaries of the reserve. In addition, the MCP method calculated similar home range sizes for both prides while the 95% UD for the Northern Pride (21.42km$^2$) was nearly half of the 95% MCP for the same pride (37.19km$^2$) and less than half the 95% UD of the Southern Pride (47.20km$^2$). The sizes of the centres of activity also differed in each method. The Northern Pride's 50% MCP (5.22km$^2$) was more than twice the 50% UD (2.71km$^2$) while the Southern Prides 50% MCP (7.45km$^2$) and 50%

UD (6.14km$^2$) were more similar. Both methods show that the Northern Pride's activity was concentrated in a smaller area than the Southern Pride.

Table 5.1. Size of home ranges and centres of activity for lions on Kwandwe as calculated by the minimum convex polygon method, and the percentage of the reserve used.

| | | Area (km$^2$) | | % of reserve | |
|---|---|---|---|---|---|
| Lion | No. of fixes | 50% | 95% | 50% | 95% |
| F1 | 158 | 12.73 | 42.93 | 9.18 | 30.94 |
| F2 | 172 | 17.77 | 54.56 | 12.81 | 39.32 |
| Cubs | 173 | 18.15 | 57.48 | 13.09 | 41.43 |
| M1 | 134 | 16.60 | 52.32 | 11.97 | 37.71 |
| M2 | 30 | 3.40 | 90.39 | 2.45 | 65.15 |

Table 5.2. Size of home ranges and centres of activity for lions on Kwandwe as calculated by the fixed kernel method, and the percentage of the reserve used.

| | | Area (km$^2$) | | | % of reserve | | |
|---|---|---|---|---|---|---|---|
| Lion | No. of fixes | 50% | 75% | 95% | 50% | 75% | 95% |
| F1 | 158 | 10.53 | 22.15 | 49.82 | 7.59 | 15.97 | 35.91 |
| F2 | 172 | 17.47 | 37.36 | 67.95 | 12.59 | 26.93 | 48.98 |
| Cubs | 173 | 12.89 | 34.54 | 65.53 | 9.29 | 24.90 | 47.23 |
| M1 | 134 | 17.44 | 38.04 | 73.27 | 12.57 | 27.42 | 52.81 |
| M2 | 30 | 8.38 | 15.49 | 54.41 | 6.04 | 11.16 | 39.22 |

Table 5.3. Size of home ranges and centres of activity for lions on Shamwari as calculated by the minimum convex polygon method, and the percentage of the reserve used.

| | | Area (km$^2$) | | % of reserve | |
|---|---|---|---|---|---|
| Pride | No. of fixes | 50% | 95% | 50% | 95% |
| Northern | 64 | 5.22 | 37.19 | 4.14 | 29.50 |
| Southern | 63 | 7.45 | 31.93 | 5.91 | 25.32 |

Table 5.4. Size of home ranges and centres of activity for lions on Shamwari as calculated by the fixed kernel method, and the percentage of the reserve used.

| | | Area (km$^2$) | | | % of reserve | | |
|---|---|---|---|---|---|---|---|
| Pride | No. of fixes | 50% | 75% | 95% | 50% | 75% | 95% |
| Northern | 64 | 2.71 | 12.14 | 21.42 | 2.15 | 9.62 | 16.99 |
| Southern | 63 | 6.14 | 20.24 | 47.20 | 4.87 | 16.05 | 37.43 |

At Kwandwe, the home ranges and centres of activity of the two females (Figure 5.2 & 5.3), the cubs (Figure 5.4) and the pride male (M1; Figure 5.5), the lions that comprise the pride, were very similar in orientation within the reserve and were located in the south-western and central parts. Both methods show that the single male (M2; Figure 5.6) ranged over a large area of the reserve but the 95% MCP suggests a greater use of the central area of the reserve than the 95% UD. A portion of the 95% MCP for M2 fell outside the reserve boundary. M2 had activity centres (50% MCP and UD) located in the north-eastern part of the reserve that were small, 3.40km$^2$ and 8.38km$^2$, in comparison to the other lions which ranged from 12.73km$^2$ to 18.15km$^2$ for the MCP method and 10.53km$^2$ to 17.47km$^2$ for the kernel method.

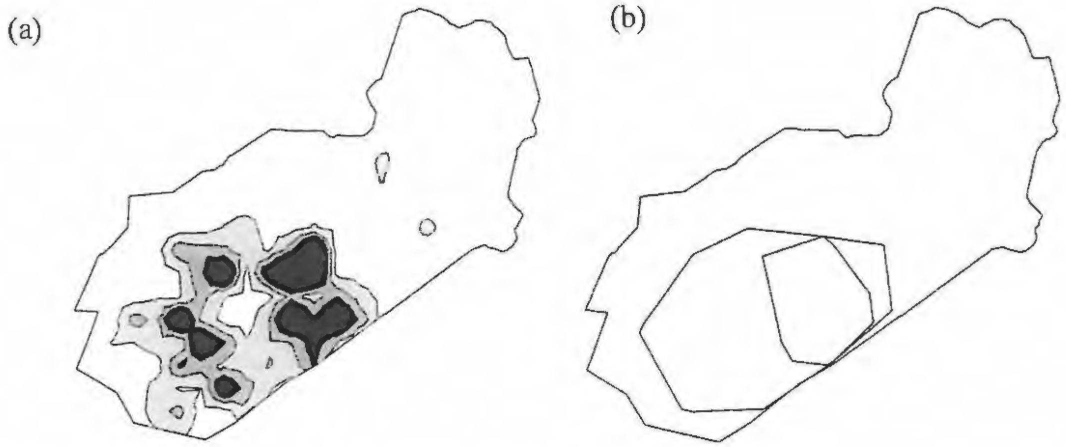

Figure 5.3. Home range and centres of activity for F1, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method. Black indicates 50% UD, medium grey 75% UD, and light grey 50% UD for this and following figures.

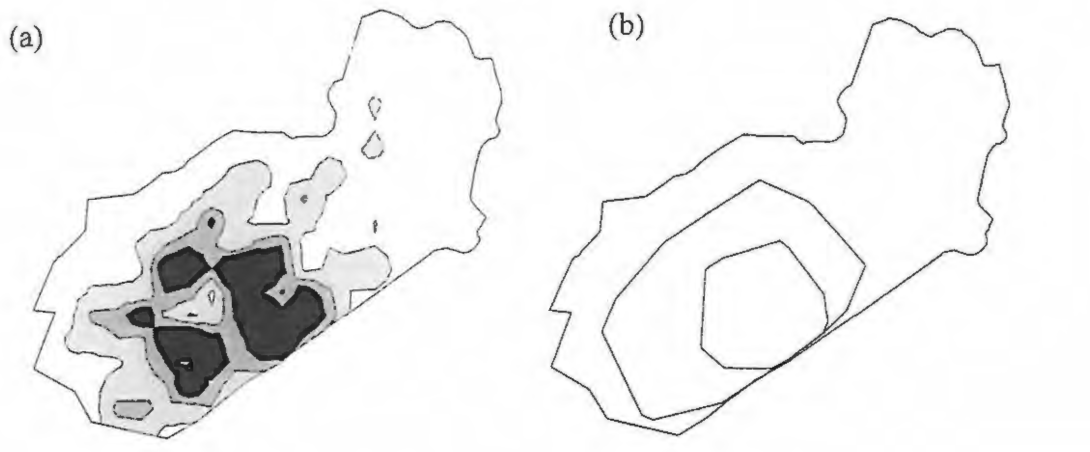

Figure 5.4. Home range and centres of activity for F2, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

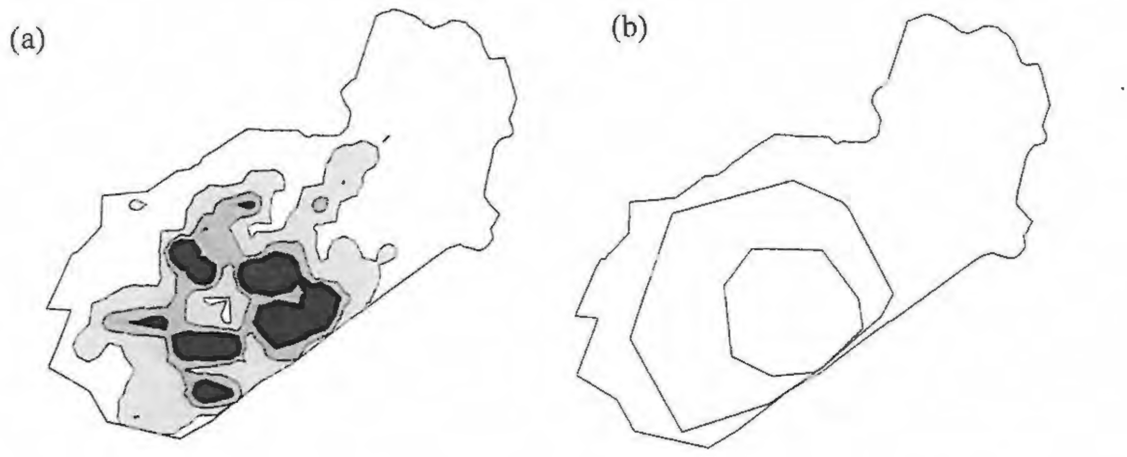

Figure 5.5. Home range and centres of activity for the cubs, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

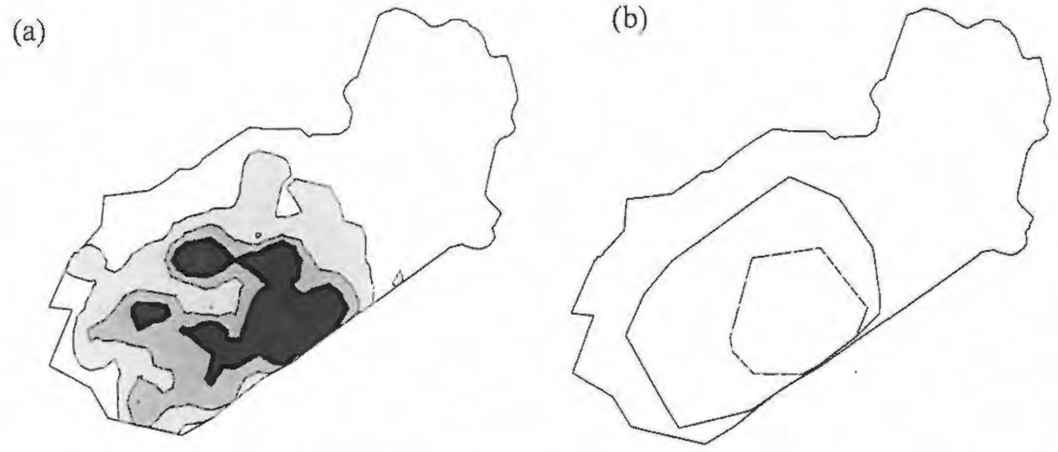

Figure 5.6. Home range and centres of activity for M1, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

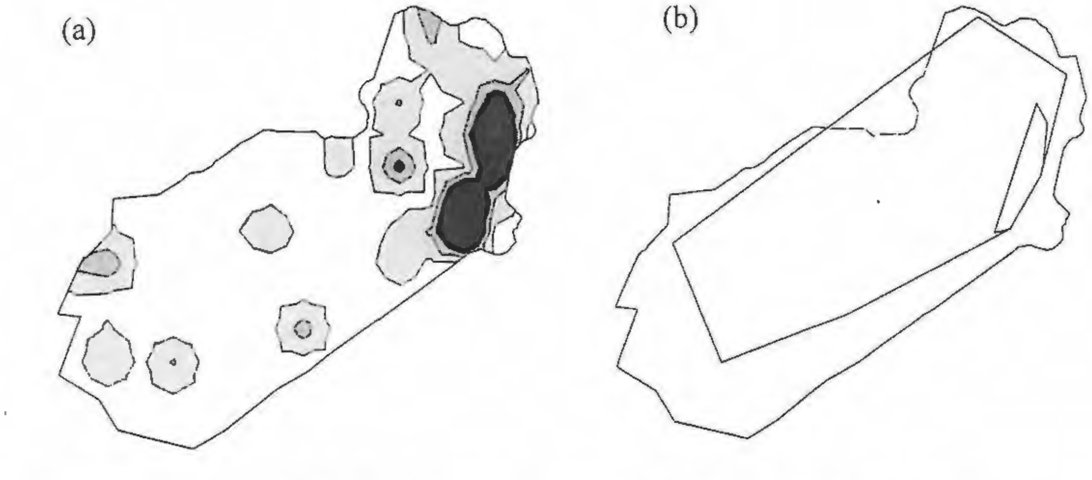

Figure 5.7. Home range and centres of activity for M2, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

*Overlap of home ranges*

In terms of overlap, the home ranges of the cubs, F2 and M1 were most similar and differed only slightly from the home range of F1. M1 and M2 appeared to exhibit typical patterns of avoidance (compare Figures 5.5 & 5.6) however the small sample size for M2 makes comparisons difficult. The home ranges of the Shamwari prides overlapped spatially, but not temporally, in the middle of the reserve (Figures 5.8 and 5.9).

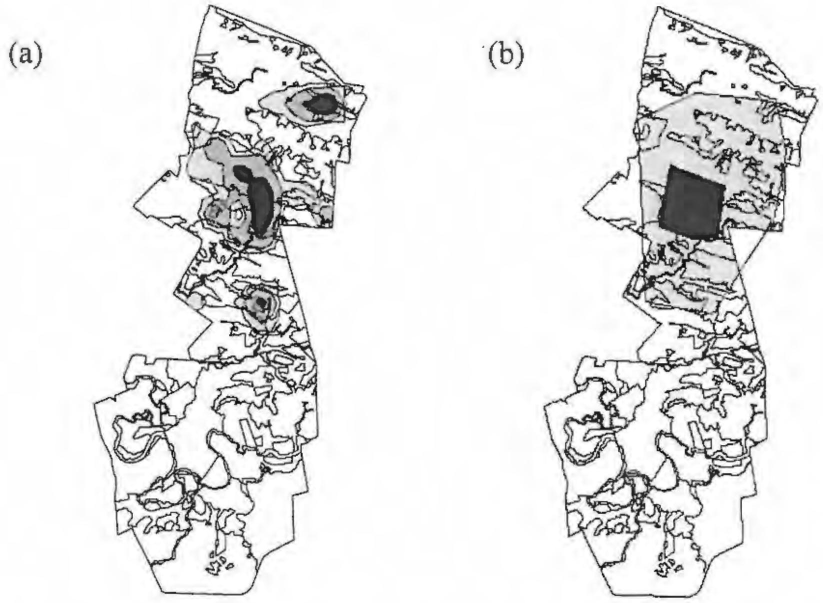

Figure 5.8. Home range and centres of activity for the Northern Pride, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

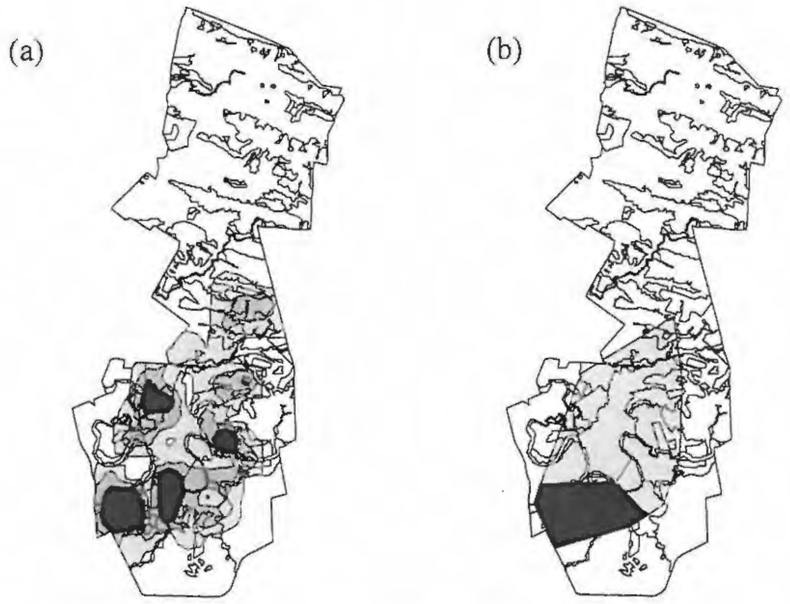

Figure 5.9. Home range and centres of activity for the Southern Pride, determined by (a) the 50%, 75% and 95% utilization distribution using the fixed kernel method and (b) the 50% and 95% minimum convex polygon method.

*Habitat selection*

At the reserve level, the null hypothesis was rejected because the observed selection of vegetation types was significantly different ($p < 0.05$) from the expected selection for all lions and prides on both reserves indicating that the lions' selection of habitat over each reserve was non-random. At Shamwari (Table 5.5), the Northern Pride showed high levels of preference for Secondary *Acacia* Thicket, Cleared Land and Montane Grassland and utilized the Subtropical Thicket areas approximately according to its availability on the reserve. Of the vegetation types utilized, the Southern Pride showed high preference for all vegetation types except Bushclump Savanna, Montane Grassland and Subtropical Thicket. Neither pride was observed using Afromontane Forest and Open Grassland areas. At Kwandwe (Table 5.6), M2 showed preferences of greater or approximately equal to one for all habitat types, with the exception of Karoo Shrubland. M2 was also the only lion to utilize the Tall *Euphorbia* Thicket and Bushclump Savanna areas. All lions, with the exception of M2, utilized the Karoo Shrubland more than expected while the Medium *Portulacaria* Thicket was utilized approximately according to availability. All other habitat types were under-utilized and, with the exception of Riverine Thicket, were not utilized by all members of the pride.

Table 5.5. Proportional availability of vegetation types on Shamwari and the preference shown by each pride for these vegetation types. Blanks indicate vegetation types where no utilization was recorded.

| Vegetation type | Availability | Northern Pride | Southern Pride |
|---|---|---|---|
| Afromontane Forest | 0.005 | | |
| Bontveld | 0.079 | 0.197 | |
| Bushclump Savanna | 0.020 | 0.784 | 0.809 |
| Calcrete Fynbos* | 0.000 | | 251.382 |
| Cleared Land | 0.017 | 3.700 | 7.638 |
| Cultivated Land | 0.129 | 0.729 | 2.008 |
| Grassy Fynbos | 0.054 | 0.290 | |
| Karoo Scrub | 0.021 | | 1.562 |
| Montane Grassland | 0.085 | 2.388 | 0.569 |
| Open Grassland | 0.045 | | |
| Primary *Acacia* Thicket | 0.060 | 0.261 | 2.694 |
| Riverine Bush | 0.029 | 0.545 | 2.250 |
| Secondary *Acacia* Thicket | 0.014 | 6.651 | |
| Subtropical Thicket | 0.442 | 1.060 | 0.620 |

* Proportional availability approximately 0.0001

Table 5.6. Proportional availability of vegetation types on Kwandwe and the preference shown by each lion for these vegetation types. Blanks indicate vegetation types where no utilization was recorded.

| Vegetation type | Availability | F1 | F2 | Cubs | M1 | M2 |
|---|---|---|---|---|---|---|
| Bushclump Karoo | 0.110 | 0.045 | 0.036 | | 0.018 | 1.655 |
| Bushclump Savanna | 0.029 | | | | | 1.517 |
| Karoo Shrubland | 0.308 | 1.627 | 1.708 | 1.711 | 1.818 | 0.399 |
| Medium *Portulacaria* Thicket | 0.372 | 1.296 | 1.180 | 1.183 | 1.094 | 1.008 |
| Riverine Thicket | 0.079 | 0.114 | 0.342 | 0.316 | 0.342 | 1.291 |
| Short *Euphorbia* Thicket | 0.075 | 0.053 | 0.040 | 0.107 | 0.053 | 1.840 |
| Tall *Euphorbia* Thicket | 0.027 | | | | | 1.370 |

At the home range level, the null hypothesis was once again rejected as the difference between habitat selection and the proportional availability of habitat types within home ranges was statistically significant ($p < 0.05$) for the 95% MCPs of F1 (Table 5.7), the cubs (Table 5.9) and M2 (Table 5.10), the 50% MCP of the cubs and the 95% UDs of all lions, indicating that the selection of habitat by these lions was nonrandom. By contrast, F2 showed no significant selection of habitat type in either estimate of home range and core areas (Table 5.8). Statistical significance could not be calculated for MCPs or UDs that contained only two habitat types. In all cases, the tendency was to use more Karoo Shrubland and less Medium *Portulacaria* Thicket than was available. Karoo Shrubland was the most utilized habitat type for all lions except M2 (Table 5.11), which used Bushclump Karoo areas more often than any other habitat type. The Tall *Euphorbia* Thicket areas were not represented in any core area or home range and Bushclump Savanna was only utilized by M2.

Table 5.7. Preference shown for vegetation types and the proportional availability of each type within the 50% and 95% MCPs and UDs of F1.

| Vegetation type | MCP | | | | UD | | | |
|---|---|---|---|---|---|---|---|---|
| | Preference | | Availability | | Preference | | Availability | |
| | 50% | 95% | 50% | 95% | 50% | 95% | 50% | 95% |
| Bushclump karoo | | | | | | 1.400 | | 0.005 |
| Bushclump savanna | | | | | | | | |
| Karoo shrubland | 0.993 | 1.113 | 0.865 | 0.573 | 1.050 | 1.222 | 0.777 | 0.501 |
| *Portulacaria* thicket | 1.044 | 0.854 | 0.135 | 0.417 | 0.825 | 0.783 | 0.223 | 0.479 |
| Riverine thicket | | 0.700 | | 0.010 | | 0.778 | | 0.009 |
| Short *Euphorbia* thicket | | | | | | 0.000 | | 0.005 |
| Tall *Euphorbia* thicket | | | | | | | | |

Table 5.8. Preference shown for vegetation types and the proportional availability of each type within the 50% and 95% MCPs and UDs of F2

| Vegetation type | MCP | | | | UD | | | |
|---|---|---|---|---|---|---|---|---|
| | Preference | | Availability | | Preference | | Availability | |
| | 50% | 95% | 50% | 95% | 50% | 95% | 50% | 95% |
| Bushclump karoo | | | | | | 0.000 | | 0.005 |
| Bushclump savanna | | | | | | | | |
| Karoo shrubland | 1.039 | 1.073 | 0.817 | 0.604 | 1.089 | 1.169 | 0.696 | 0.526 |
| *Portulacaria* thicket | 0.825 | 0.861 | 0.183 | 0.373 | 0.796 | 0.809 | 0.304 | 0.439 |
| Riverine thicket | | 1.240 | | 0.025 | | 1.071 | | 0.028 |
| Short *Euphorbia* thicket | | | | | | 0.000 | | 0.002 |
| Tall *Euphorbia* thicket | | | | | | | | |

Table 5.9. Preference shown for vegetation types and the proportional availability of each type within the 50% and 95% MCPs and UDs of the cubs.

| Vegetation type | MCP | | | | UD | | | |
|---|---|---|---|---|---|---|---|---|
| | Preference | | Availability | | Preference | | Availability | |
| | 50% | 95% | 50% | 95% | 50% | 95% | 50% | 95% |
| Bushclump karoo | | | | | | | | |
| Bushclump savanna | | | | | | | | |
| Karoo shrubland | 1.046 | 1.118 | 0.834 | 0.620 | 1.104 | 1.261 | 0.703 | 0.524 |
| *Portulacaria* thicket | 0.780 | 0.782 | 0.164 | 0.353 | 0.754 | 0.694 | 0.297 | 0.438 |
| Riverine thicket | 0.000 | 1.148 | 0.002 | 0.027 | | 1.036 | | 0.028 |
| Short *Euphorbia* thicket | | | | | | 0.667 | | 0.009 |
| Tall *Euphorbia* thicket | | | | | | | | |

Table 5.10. Preference shown for vegetation types and the proportional availability of each type within the 50% and 95% MCPs and UDs of M1.

| Vegetation type | MCP | | | | UD | | | |
|---|---|---|---|---|---|---|---|---|
| | Preference | | Availability | | Preference | | Availability | |
| | 50% | 95% | 50% | 95% | 50% | 95% | 50% | 95% |
| Bushclump karoo | | | | | | 0.000 | | 0.002 |
| Bushclump savanna | | | | | | | | |
| Karoo shrubland | 0.999 | 1.028 | 0.804 | 0.602 | 1.046 | 1.116 | 0.703 | 0.545 |
| *Portulacaria* thicket | 1.000 | 0.936 | 0.197 | 0.373 | 0.892 | 0.856 | 0.297 | 0.423 |
| Riverine thicket | | 1.280 | | 0.025 | | 1.148 | | 0.027 |
| Short *Euphorbia* thicket | | | | | | 0.000 | | 0.004 |
| Tall *Euphorbia* thicket | | | | | | | | |

Table 5.11. Preference shown for vegetation types and the proportional availability of each type within the 50% and 95% MCPs and UDs of M2.

| Vegetation type | MCP | | | | UD | | | |
|---|---|---|---|---|---|---|---|---|
| | Preference | | Availability | | Preference | | Availability | |
| | 50% | 95% | 50% | 95% | 50% | 95% | 50% | 95% |
| Bushclump karoo | 0.806 | 3.872 | 0.798 | 0.086 | 1.195 | 1.566 | 0.502 | 0.198 |
| Bushclump savanna | | 4.111 | | 0.018 | | 1.533 | | 0.045 |
| Karoo shrubland | | 0.180 | | 0.411 | 0.000 | 0.888 | 0.016 | 0.116 |
| *Portulacaria* thicket | | 0.892 | | 0.249 | 3.190 | 0.767 | 0.021 | 0.360 |
| Riverine thicket | | 0.841 | | 0.088 | 0.000 | 0.663 | 0.174 | 0.104 |
| Short *Euphorbia* thicket | 1.767 | 1.982 | 0.202 | 0.112 | 1.156 | 1.237 | 0.288 | 0.139 |
| Tall *Euphorbia* thicket | | 0.000 | | 0.036 | | 0.000 | | 0.038 |

## DISCUSSION

One of the reported problems with the MCP method is that it includes unused areas and thus tends to overestimate home ranges. In the present study, this was seen for the nomadic male (M2) at Kwandwe where the 95% UD was nearly 50% of that generated by the MCP, and the Shamwari lions, with the exception of the Southern Pride for which the 95% UD was greater than the 95% MCP. In most other cases the areas calculated by the two methods were similar and, particularly at the 50% level the kernel method resulted in larger areas. One of the possible explanations for this is the relative sample sizes. Where sample sizes were low, such as for M2, there were greater differences between the estimates of home range and centres of activity generated by each method. It is recommended that the kernel-based method be used to determine home ranges and activity centres, particularly where sample sizes are small.

Home ranges of lions in Shamwari and Kwandwe were substantially smaller than has been generally reported for lions (see Appendix D). An exception is the study of reintroduced lions in Phinda Resource Reserve (Hunter 1998), where home ranges were calculated using ArcView 3.0 software, the 95% MCPs varied from 27.56km$^2$ for a lone female to 130.20km$^2$ for a coalition of three males. Core areas (50% MCPs) in Phinda averaged 6.78km$^2$ for females and 15.18km$^2$ for male coalitions. A second exception is a study in the Savuti region in Chobe (Viljoen 1993) where, using the harmonic mean measure, home ranges of 42km$^2$ to 369km$^2$ were calculated, with an average of 217km$^2$ and average core areas (50% isopleths) of 29km$^2$ and 45km$^2$ for the rainy and dry seasons respectively. Phinda is comparable to Kwandwe and Shamwari since it is a small reserve (170km$^2$) where, at the time of Hunter's (1998) study, thirteen adult lions had been introduced and the biomass of eight of the ten most important prey species was 1996.3kg.km$^{-2}$ (2300kg.km$^{-2}$ for Shamwari and 4800kg.km$^2$ for Kwandwe). The Savuti region Chobe, on the other hand, is an area of 300km$^2$ in a reserve of 11 700km$^2$ with an average of 87 lions occurring in the study area. The average increase in home range size from 136km$^2$ in the rainy season to 217km$^2$ in the dry season for lions in Chobe (Viljoen 1993) can be attributed to a concurrent decrease in herbivore biomass from 2119kg.km$^{-2}$ to 730kg.km$^{-2}$ in the Savuti region, which resulted in wider foraging by lions. The smaller range sizes estimated in the present study can be attributed to a combination of small pride size, high prey to lion biomass on the reserves, the sedentary nature of prey and the restrictive boundaries of the reserve.

Macdonald (1983) plotted data from eight studies of lions and found that there was a significant positive correlation between group size and home range size ($r = 0.70$; $p < 0.02$). Group size is limited by the availability of prey while home range size is determined by the dispersion of resources. In addition, the costs of patrolling and defending a territory and the advantages of knowing a home range well means that an animal will favour home ranges that are as large as necessary but as small as possible (Macdonald 1983). Studies have shown that, in areas such as Chobe, where ungulate species are migratory, lion home range sizes change seasonally as prey abundance fluctuates (van Orsdol *et al.* 1985; Stander 1991; Viljoen 1993, Stander 1997). Regardless of whether prey are migratory or resident, home range sizes are generally inversely correlated with prey densities (Ogutu & Dublin 2002) as lions have to forage further in search of food. Long-term changes in range size have been observed in prides inhabiting the woodland and woodland/plains habitats in the Serengeti as well as prides in Ngorongoro Crater (Van Orsdol *et al.* 1985). Significant long-term changes in range size are to be expected in small reserves where space is a limiting factor and populations are growing, especially for males that may gain or lose tenure of a pride and adapt their home ranges accordingly. It is possible that pride ranges will become smaller, as was found by van Orsdol *et al.* (1985) in their review of home range size, and increased overlap between home ranges may occur. However, without any long-term studies based specifically in small reserves it is difficult to do more than speculate on future use of space and habitat types by lions on either Shamwari or Kwandwe. It is almost certain, however, that aggressive interactions between males and between different prides will increase, as will interspecific competition and aggression shown towards other carnivores. Although not analysed here due to insufficient data, the two males in Shamwari appear to move throughout the reserve and were regularly seen fighting. There still appears to be space available for Shamwari's lion populations to grow but their use of this space will be influenced by social structure and social dynamics. The present data will serve as a base against which future changes can be monitored, and possibly the starting point of a long-term monitoring project in which the effects of changes in lion population size and structure on habitat selection and utilization are examined.

The differences in the home ranges and core areas of the two females in Kwandwe illustrate the fission-fusion nature of prides. F1 spent some time away from F2 and the cubs in the second half of 2003. The large home range and small core size of M2 is typical of the nomadic nature of non-territorial males. The two males on Kwandwe utilized different parts of the reserve, and between them almost the entire reserve was utilized. This suggests that if the new cubs do not form a coalition with M1, their father, a competition for space might arise. On the other hand, if they do form a coalition, it is unlikely that they will lose tenure of the pride to a single male (Bygott *et al.* 1979), which will result in matings between mother and son or sister and brother. This situation leads to inbreeding and the problems associated with it (see Chapter 1). Both males on Shamwari have been seen mating with females from both prides and since the males are unrelated, the chance of inbreeding, while still a major consideration in the management of Shamwari's population, is lower than for Kwandwe.

Lions may select particular vegetation types for a number of reasons, including the distribution and type of prey available, the amount of cover available for stalking, the availability and spacing of suitable den sites, the availability of water and the amount of cover available for lying up during the day. On Shamwari the two prides selected vegetation types within the part of the reserve where they were initially released (see Chapter 2). Vegetation cover is an important variable in the hunting success of lions (Schaller 1972; van Orsdol 1984; Funston *et al.* 2001), with the highest success rate occurring in long grass and dense shrub, particularly at night. In Phinda Resource Reserve, where lions were able to select between long grass and dense shrubs, lions showed greater than expected selection of grassland and less than expected selection of dense vegetation types (Hunter 1998). However, lions appear to show a high degree of behavioural plasticity and respond to prevalent ecological conditions (Funston *et al.* 2001). This is illustrated in Kwandwe, which has very few areas of open grassland and is dominated by areas of dense vegetation. Within these dense vegetation types, Medium *Portulacaria* Thicket (37.2%) and Karoo Shrubland (30.8%) dominate the reserve in terms of relative area and were most utilized by the pride and M1. The selection of these habitat types was most likely due to the cover they afforded for hunting and for resting during the day when lions are generally inactive. Male lions hunting alone are more successful in dense vegetation than more open habitat (Funston *et al.* 2001) which explains M2's preference for areas such as Bushclump Karoo, Bushclump Savanna and Short *Euphorbia* Thicket. Tall *Euphorbia* Thicket and Bushclump Savanna are found on the slopes of hills and in high lying areas of the reserve respectively, which may explain the under-utilization of these habitat types in relation to their availability. In addition, Tall *Euphorbia* Thicket can be compared to forest or dense woodland areas in terms of structure, and these areas may be avoided by lions (and many of their prey species) in favour of more open areas where hunting success is likely to be higher and more prey species can be found (Funston *et al.* 2001). Riverine Thicket is also similar in structure to forest, which would explain the under-utilization of this habitat type.

In Shamwari, Bontveld, Grassy Fynbos and Secondary *Acacia* Thicket were not utilized by the Southern Pride and Calcrete Fynbos and Karoo Shrubland, were not used by the Northern Pride and were not included within the pride's home range. Neither pride was observed using Afromontane Forest and Open Grassland areas, probably because Afromontane Forests occurs in patches, particularly in deep kloofs or in steep gullies which are inaccessible to both lions and vehicles (O'Brien 2000) and the Open Grassland has very little woody growth and little to no variation in topography which limit the cover available for hunting lions. Subtropical Thicket, situated predominantly on sloping ground (O'Brien 2000) was the vegetation most utilized, in terms of the number of observations, by both prides and is the most abundant habitat type on the reserve. Subtropical Thicket provides ideal cover for hunting lions and allows lions to stalk close to their prey before being detected. The majority of kills by lions in Shamwari were kudu (see Chapter 3), which, as browsers, were especially abundant in these thickets. However the preference for this vegetation type was lower than expected for the Southern Pride and approximately equal to availability for the Northern Pride, which suggests that the lions were not showing a preference for Subtropical Thicket but using the habitat type at random. The Southern and Northern Pride showed strong preferences for Primary and Secondary *Acacia* Thickets respectively which are structurally similar and provide the ideal type of cover for stalking lions. As with the Subtropical Thicket areas, *Acacia*

Thickets also support high abundances of prey species such as kudu. The exceptionally high preference of 251.382 for Calcrete Fynbos by the Southern Pride is an artifact of the size of the vegetation type (0.008km$^2$). Only one observation of the pride utilizing this area was made. There was a higher than expected use of Cleared Land and Montane Grassland by the Northern Pride and of Cleared Land and Cultivated Land by the Southern Pride. These vegetation types do not provide a great deal of cover for stalking lions, therefore the apparent preference for these areas may have been the result of three factors. Firstly, lions often chase thicket-dwelling prey out into the open before killing them and as a result the carcasses are found in open areas despite the fact that the hunt began in the thicket. Secondly, these areas have a high abundance of grazing herbivores such as wildebeest and blesbuck, which are two of the important species in the diet (see Chapter 3). These species are highly visible on the open plains, which may explain the lions' preference for the species and the habitat type. Thirdly, carcasses will be more visible in these areas and, since the habitat selected is based on GPS fixes of kills there will be bias in the observed selection. This bias illustrates the problems associated with opportunistic sightings of lion kills and the importance of collecting GPS fixes for lion sightings as well as their kills. It is likely that the preference for the open areas shown by the kill data is a combination of these three factors.

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# CHAPTER 6

## General discussion and management implications

The increasing demand for land by people means that the opportunity for conserving large, contiguous areas in South Africa is diminishing, while the influx of tourists to the country is encouraging the formation of small, enclosed reserves. The size of these reserves and their function as tourist destinations, make management difficult and this is aggravated because most of the research on African ecosystems has been done in large reserves and open systems (Kruuk & Turner 1967; Schaller 1972; Saba 1979; Heinsohn 1997; Funston *et al.* 1998). Although it can be argued that small populations do not add anything to the conservation of a species on a large scale, these unique systems may one day be very important in the conservation of both predator and prey species, and small populations must therefore be managed effectively in order to maintain healthy and viable metapopulations (see Chapter 1). While lions are not rare or endangered, it is a species that can have a major impact on populations of smaller predators and prey, particularly when space is limited and few areas exist that can act as refuges. This study looked at the diet, the condition of the prey and the selection of habitat and use of space by lions when restricted to small, closed reserves with the aim of improving the understanding of the behavioral ecology of lions within these systems, which in turn will contribute to better management of lions on small reserves.

The dietary analysis showed that the lions killed mostly large (>120kg) animals, more adults than juveniles and subadults, and more males than females (see Chapter 3). These findings are similar to what has been reported for lions elsewhere (Schaller 1972; Rudnai 1974; Ruggiero 1991; Stander 1992; Owen-Smith 1993; Viljoen 1997; Funston *et al.* 1998, 2001) and may therefore be applicable to other reserves, regardless of size. The lions preferentially selected some species, such as wildebeest, ostrich and warthog, while others, such as bushbuck, springbuck and duiker, were killed in proportions below their relative abundances. It appears that, when presented with an unusually high abundance of prey, particularly prey that were initially naïve to predators, lions at Shamwari hunted more than they required to meet their daily intake needs. This behaviour has been documented by other researchers (see Packer *et al.* 1990; Stander 1991), but in most cases hunting more than required to meet daily needs has been linked to seasonal increases in prey biomass. In small reserves, prey abundances are likely to fluctuate relatively little in response to seasonal changes since prey animals in this situation do not have refuges or the option of escape from predation through migration. While the "predator regulation" hypothesis suggests that lions can keep the numbers of herbivores below starvation level thereby maintaining healthy prey populations (Sinclair & Arcese 1995), it is questionable whether this will apply in small reserves since the lack of refuges for ungulates or natural source populations means that lions are able to hunt a population until it can no longer recover without intervention. If the lions continue to select a small number of species and kill more than they require, they will ultimately affect the management of the reserve because either prey populations will have to be increased or lion numbers will have to be reduced. One of the major factors that must be taken into consideration when a population is reduced through predation or removal from the reserve, is that lower numbers, particularly of carnivores, will mean fewer sightings and this will reflect on the attraction of the reserve to the foreign tourist market.

Knowledge of the feeding habits, in terms of species selected, of a population of lions is useful since it allows the calculation of estimated removal of animals from the system. However, the calculation of annual offtake in itself does not tell the whole story, and the age, sex and condition of the animals killed allows a more refined analysis of the possible effects of lion predation on the ungulate populations. One of the greatest impacts lions can have on prey populations is through the removal of prime reproductive animals and it is therefore necessary to examine the condition of the animals killed by lions. From the dietary analysis, it appears that the lions were taking more adults than juveniles or subadults, and this will affect the reproductive output of the population. On the other hand they killed slightly more males than females, and males are less important in polygynous mating systems (Mysterud *et al.* 2002). Assessment of the condition of animals killed by lions at Kwandwe showed that, overall, they selected animals in moderate to good condition, although gemsbok and kudu kills were in moderate to poor condition (see Chapter 4). Whether or not this reflects the condition of the population is not known and highlights the need to know both the condition of individual prey items and the condition of the prey population. Thus it is not possible to say whether the lions are killing the fittest prey, which means that it is difficult to predict the effect of predation on the reproductive output of the prey population. If the level of condition of the population drops and the lions continue to select the healthy individuals then their impact on the prey population will be greater. MFI is a useful tool since it is an easy and cost-effective method of evaluating animal condition and will allow managers to better predict the effect of predation on the ungulates in the system.

Apart from the lions' use of food resources, it is also important to examine their use of habitat and space. The home range analysis showed that the home ranges and centres of activity of the lions on both reserves were small relative to other studies, but that they utilized the majority of the reserve area, particularly in Kwandwe (see Chapter 5). The lions showed a preference for certain vegetation types in both reserves while avoiding others, reflecting a pattern of habitat use that was similar to what has been reported previously (Funston *et al.* 2001). Understanding the use of vegetation types and space by lions within a reserve means that if that reserve increases in size, it will be possible to determine the area that is suitable for lions and therefore the increase in the lion population that can be allowed. The effect of increased lion populations, particularly males, is not known but increased conflict between individuals and between lions and other carnivores can be expected (see Chapter 1). It is also important to monitor the use of habitat and space by other carnivores since keeping the lion population constant while increasing the area of the reserve may provide additional space and refuge areas for the subordinate predators such as cheetah, thereby reducing conflict.

The three aspects of the behavioural ecology of lions addressed in this study are interlinked and an attempt has been made to model the predator prey system using the program Vensim. Separate, independently functioning sub-models were designed for the lions and the herbivores to examine the sensitivity of the model to different variables. The herbivore sub-model included prey and non-prey species that competed for food resources but were not constrained or affected by predation. The lion sub-model looked at the growth of lion populations when the food availability was limited to their daily intake requirements, and assumed that prey was evenly distributed in space and that the "resource" was never exhausted. However, when the two models were combined so that they became dependant on one another, the outputs were unrealistic. This was largely due to the inability to apply carrying capacities or minimum population values to the model. Nevertheless, building the model afforded valuable insight into the main factors that affect the growth or decline of a population. There are many variables that can be factored in to a greater or lesser extent and some variables are more difficult to model than others. The flow diagrams in Figures 6.1-6.3 include some factors, the role of refuges in the use of space and avoidance of predators by prey species, for which there are no long-term data that can provide insight into the responses of predators and prey to changes in these variables, but which are nonetheless important in the dynamics of the system. Figures 6.1 and 6.2 show the factors that directly affect the lions and their prey respectively, while Figure 6.3 shows how, when combined, the lions and their prey affect each other.

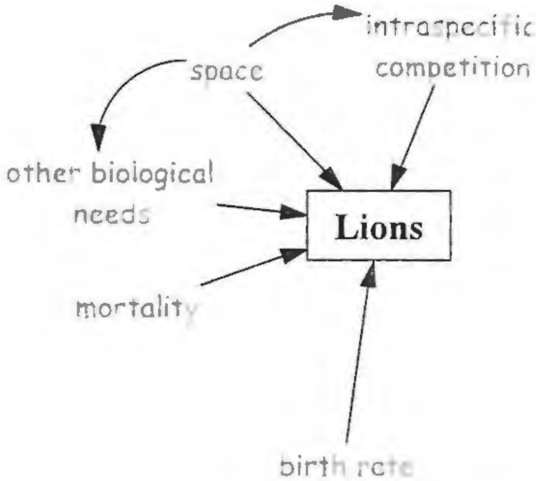

Figure 6.1. Flow diagram of the lion population sub-model to show the factors affecting the population.

Intrinsic to the lion sub-model is the age and sex structure of the population since the number of reproductively active females in the population will affect the growth of that population. The factors that ultimately will affect the growth or decline of a lion population are birth rates and mortality rates. 'Birth rates' were assumed to remain fairly constant under conditions where resources are not limited. 'Mortality' includes natural senescence, disease and fatal injuries sustained during hunts. Deaths resulting from aggressive encounters between lions and infanticide are included with 'intraspecific competition'. 'Other biological needs' includes factors such as access to water and the availability of suitable den sites. Space is a requirement for any animal and in the case of the lions, this space is the minimum area required to establish a territory whereby intraspecific competition is at a minimum, and the costs of defense of the area is balanced by the gains in terms of food resources and other biological needs, such as den sites and water availability. In the lion sub-model, it is assumed that there is sufficient prey to meet the daily intake requirements of the population and that prey are evenly distributed through space.

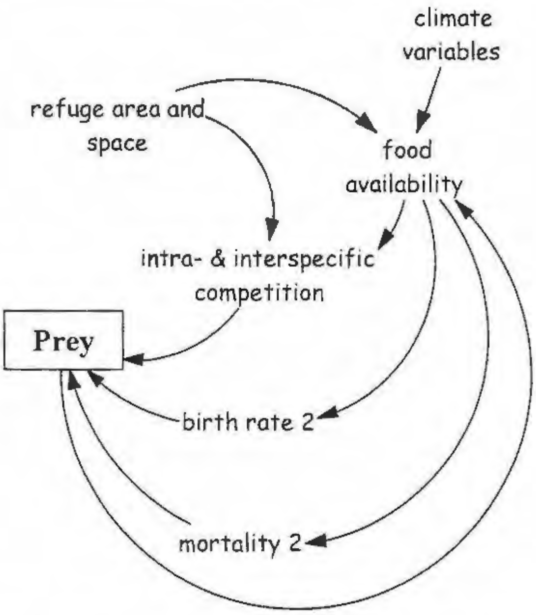

Figure 6.2. Flow diagram of the prey population sub-model to show the factors affecting the population.

The prey population includes all herbivore species on a reserve from which a population of lions can select its prey. For the prey population without predators, 'food availability' is the pivotal factor affecting population growth. The availability of food is affected by climate variables such as rainfall and temperature. This in turn affects the 'birth rate' since, when food becomes limited, the level of fecundity will decrease. Food also affects 'mortality', especially in times of drought when animals may die of malnourishment or become more susceptible to disease. As populations grow, 'intra- and interspecific competition' will increase between animals that utilize the same resource. Once again, this competition will be exacerbated in times when food is scarce. Prey populations are also affected by the availability of space and this is particularly true for territorial species that defend and maintain home ranges. It is important to note at this point that, in both sub-models, almost all factors feed back into the model to a greater or lesser degree but only the most important are shown here. For example, while food availability affects the growth of the prey population, this increase or decrease will place more or less pressure on resources and will result in increase or decrease in food availability. At one extreme, overstocking of prey species in a small reserve particularly during a period of drought could result in deterioration of the vegetation such that even a period of high rainfall will not restore the food supply, although it may alleviate food stress temporarily. On the other hand, herbivores may improve their food source through grow stimulation as a result of grazing and by fertilization and seed dispersal through droppings.

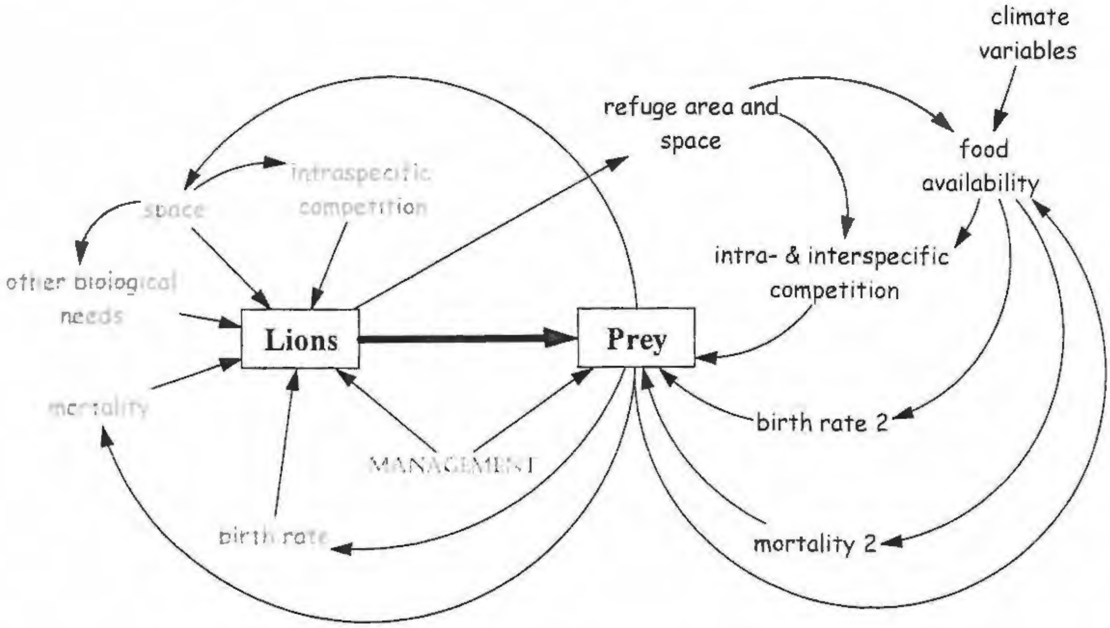

Figure 6.3. Flow diagram showing the main factors affecting lions and prey populations when the two sub-models are combined. Green indicates those factors that directly affect lions and blue indicates those factors that directly affect the prey population. The red factor is a variable that has an important effect of both lions and prey.

When the two models are combined, the predators and prey begin to affect each other. This is more complex than a simple reduction in numbers of prey since lions will only prey on certain species, which affords other species the opportunity to gain a competitive advantage as more food and space becomes available. The way the lions select prey in terms of age, sex and condition of the animals will also affect the growth of the prey population. Changes in the size of the lion population will result in a change in the availability of refuge areas for the prey. As lion populations grow, particularly in these small reserves where space is limited, areas of refuge may be reduced until herbivores are unable to escape predation by moving to new areas or through an annual migration. This is illustrated in large open systems like the Serengeti where ungulates migrate during wet and dry seasons in search of food and water. In the Serengeti system this ultimately affects the predators, which adapt their home ranges by expanding them when the migratory species leave the area, or by following the migration. Prey also affect the lions' use of space in small reserves but since no migration can occur, territories will tend to be large when the over-all prey density is low and small when prey densities are higher. This, in turn, will affect the intraspecific competition between lions as they encounter each other more or less often. Prey can also affect birth and mortality rates of the carnivore since a decrease in prey biomass will result in an increase in mortality, decreased cub survival and reduced fecundity.

Human intervention through management is a key factor that will affect both prey and predators and can potentially change the dynamics of this system. Management can take a number of forms, for example the control of predator and prey numbers by removal of animals for sale or culling, or through the addition of new animals; addition of new land and therefore resources; through the contraception of lions or the manipulation of pride sizes and sex structure; and through the reintroduction of other predators which place greater stress on the prey population.

An effective management system is one that, as far as possible, anticipates problems rather than continually corrects mistakes, and the anticipation of problems requires a good monitoring system built around accurate and reliable collection of information. The problems with incomplete data are illustrated by the unreliable estimates of annual offtake for year 3 of the Shamwari data (see Chapter 3) and the effect of small sample size on the calculations of home range area (see Chapter 5). The removal of radio collars and failure of internal transmitters meant that the lions in Shamwari were more difficult to monitor, particularly in the dense vegetation that is common to areas such as the Eastern Cape Province. Since reserves are primarily concerned with ecotourism, the lions are often only located for the benefit of the guests, and to ensure that the lions are healthy and have not escaped the reserve boundaries. However, detailed information on the diet of the lions and their habitat use is vital if the reserve wants to improve its management of both lions and other animals. Thus there is a conflict between the need to keep radio collars on the lions so as to ensure accurate and reliable collection of information, and the interest of the tourists who do not want to see lions with radio collars. Rangers and staff should be trained to collect and maximise information obtained from opportunistic sightings according to a standard method, for example rangers or staff can be taught how to age and sex prey animals reliably. The data can then be pooled into a central database making analysis comparatively simple. Because gaps in the observations of kills will always occur, it is recommended that a subset of data be used with an adequate maximum interval between kills (see Chapter 3). Although lions can go weeks without food, this is only under extreme circumstances and an interval of five days is recommended. This study provides a method for determining annual offtake based on the lions' daily intake requirements and the prey biomass on the reserve (see Chapter 3). Although this method is sometimes imprecise at a species level, it can provide useful predictions of total offtake. It also gives an idea of the species that are being selectively hunted and may require monitoring. Once the offtake model has been developed, it can be used to predict the effect of an increased number of lions or planned decreases in prey biomass. For example, Kwandwe are planning to decrease their herbivore biomass substantially in response to the expected period of drought and the effects of this on the lion population can be evaluated using the offtake model.

A well maintained and continuous monitoring system will not only provide information on the diet of the lions and how this is affecting the prey populations, but also on aspects of their behaviour such as interactions between individual lions as populations increase, and between lions and other carnivores. In this way potential conflict areas can be identified that can be incorporated into a management plan for the addition and removal of lions and other carnivores. For example, an understanding of the potential for coexistence among large carnivores species is vital if these reserves intend to maintain multi-carnivore systems. Lions and cheetah have a documented tendency to avoid each other spatially and temporally but this may be confounded by the enclosed nature and lack of refuges in small reserves. In addition, the conservation of highly endangered species such as cheetah may depend on these small reserves and the intense interaction between lions and smaller carnivores can be detrimental to these conservation efforts. An understanding of the social dynamics of the lions on a reserve is important when considering efforts to maintain genetic diversity (see Chapter 1). Although lions have been, and will continue to be, removed from the reserves when they reach suitable age, removal is disruptive to the social dynamics of the populations as a whole. To prevent inbreeding depression additional animals need to be brought in and once again the social consequences need to be evaluated. In small reserves, as a lion population grows, lions will come into contact with each other more regularly than on larger reserves and the possibility of aggressive interactions will be greater because natural dispersal by subadults from their native range (see Schaller 1972) is highly restricted. Introducing a single male when the prides belong to coalitions of males, will not solve the problem of inbreeding unless the new lion on his own is capable of taking over the pride, which is unlikely. This is especially true when a subadult male is introduced since adult males may exert dominance over younger males, and this must be borne in mind when deciding on the appropriate age of a reintroduced animal.

In conclusion, small reserves, although clearly unnatural systems, offer the opportunity to gain insight into aspects of lion behaviour. Ecosystems are dynamic, and the enclosed nature of small reserves may exaggerate the effects of change. Key questions that need to be answered include the effects that seasonal change in climate, droughts, and changes in reserve size, lion numbers and prey numbers can have on resource use, habitat selection and the condition of prey of lions. Therefore, there is a need not just for post-release monitoring of lions, but also for long-term monitoring. The view of predators as drawcards, forces reserve managers to attempt to accommodate more than one species of carnivore within a small reserve. The interactions between these carnivores will be intensified compared to interactions occurring in larger reserves, and more easily monitored since populations are small and animals are individually known. An understanding of these dynamics will allow reserves to determine which combinations of carnivore species can be reintroduced to a small reserve, and the aspects of biology, such as population size and demography, that could be manipulated in order to minimize conflict both within and between species. By continually monitoring populations using a standard system, reserves can determine the long-term effects of decisions made regarding predators and prey and thus improve their management system. The aim of all future research, whether by scientists or reserve staff, should be to improve knowledge in a way that will assist in the management and, ultimately, the protection of lions, their prey and other carnivores.

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# APPENDIX A

## Common and scientific names of species mentioned in the text

### CLASS MAMMALIA

**Order Carnivora**

| | |
|---|---|
| African wild dog | *Lycaon pictus* |
| Black-backed jackal | *Canis mesomelas* |
| Brown hyaena | *Hyaena brunnea* |
| Cheetah | *Acinonyx jubatus* |
| Coyote | *Canis latrans* |
| Leopard | *Panthera pardus* |
| Lion, African | *Panthera leo* |
| Lion, Asiatic | *Panthera leo* ssp. *Persica* |
| Lion, mountain | *Puma concolor* |

**Order Perissodactyla**

| | |
|---|---|
| Zebra, Burchell's | *Equus burchelli* |

**Order Artiodactyla**

| | |
|---|---|
| Blesbok | *Damaliscus dorcas phillipsi* |
| Buffalo | *Syncerus caffer* |
| Bushbuck | *Tragelaphus scriptus* |
| Caribou, barren-ground | *Rangifur tarandus* |
| Deer, mule | *Odocoileua hemionus* |
| Deer, red | *Cervus elaphus* |
| Duiker, common | *Sylvicapra grimmia* |
| Eland | *Taurotragus oryx* |
| Gemsbok | *Oryx gazella* |
| Giraffe | *Giraffa camelopardalis* |
| Hartebeest, red | *Alcelaphus buselaphus* |
| Hartebeest, Coke's | *Alcelaphus buselaphus cokei* |
| Impala | *Aepyceros melampus* |
| Kudu | *Tragelaphus strepsiceros* |
| Nyala | *Tragelaphus angasii* |
| Reedbuck | *Redunca arundinum* |
| Roan antelope | *Hippotragus equinus* |
| Sable antelope | *Hippotragus niger* |
| Springbok | *Antidorcas marsupialis* |
| Tsessebe | *Damaliscus lunatus* |
| Warthog | *Phacochoerus aethiopicus* |
| Waterbuck | *Kobus ellipsiprymnus* |

| | |
|---|---|
| Wildebeest, black | *Connochaetes gnu* |
| Wildebeest, blue | *Connochaetes taurinus* |
| **Order Primates** | |
| Vervet monkey | *Cercopithecus aethiops* |
| **Order Rodentia** | |
| Porcupine | *Hystrix africaeaustralis* |
| **CLASS AVES** | |
| Ostrich | *Stuthio camelus* |
| Goose, Egyptian | *Alopochen aegyptiacus* |

# APPENDIX B

## Daily intake rates from previous studies of lion feeding biology

| Intake (kg/FEQ/day) | Location | Source |
|---|---|---|
| 5.7 | Chobe (Savuti area) | Viljoen 1993 |
| 5 | Serengeti | Schaller 1972 |
| 6.6 | Ngorongoro Crater | Elliot & McTaggart Cowan 1978 |
| 11.35 | Etosha | Stander 1991 |
| 8.5 | Serengeti | Packer *et al.* 1990 |
| 4.3 | Mabula Game Reserve, South Africa | Power 2003 |
| 5.97 | Umfolozi Game Reserve, South Africa | Green *et al.* 1984 |
| 4.93 |  | Kruuk & Turner 1967 |
| 5.3 | Kruger | Funston *et al.* 1998 |
| 6.4 | 6 combined areas | Van Schalkwyk 1994 |
| Average | 7.12kg/female/day |  |

# APPENDIX C

## Calculation of preference indices

Table 1. The preference indices for species killed by lions on Shamwari for each year of the study period and the overall preference indices, using the full data set. Size is Small (S), Medium (M) or Large (L) as in Table 3.1.

| | COUNTS | | | | | ALL KILLS | | | | PREFERENCES | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **2000** | **2001** | **2002** | **2003** | **Ave** | **2001** | **2002** | **2003** | **Ave** | **Year 1** | **Year 2** | **Year 3** | **Overall** |
| Mountain Reedbuck | 275 | 300 | 350 | 350 | 333 | 2 | 0 | 0 | 2 | 0.24 | 0.00 | 0.00 | 0.08 |
| Impala | 465 | 694 | 600 | 852 | 715 | 2 | 4 | 4 | 10 | 0.10 | 0.24 | 0.27 | 0.19 |
| Duiker | 900 | 900 | 900 | 850 | 883 | 2 | 8 | 3 | 13 | 0.08 | 0.32 | 0.20 | 0.20 |
| Springbok | 295 | 257 | 220 | 153 | 210 | 1 | 3 | 1 | 5 | 0.14 | 0.50 | 0.37 | 0.33 |
| Bushbuck | 750 | 750 | 900 | 950 | 867 | 8 | 18 | 5 | 31 | 0.38 | 0.73 | 0.30 | 0.49 |
| Waterbuck | 60 | 65 | 65 | 62 | 64 | 1 | 0 | 3 | 4 | 0.55 | 0.00 | 2.77 | 0.86 |
| Blesbuck | 347 | 305 | 340 | 243 | 296 | 18 | 7 | 2 | 27 | 2.12 | 0.75 | 0.47 | 1.26 |
| Zebra | 60 | 84 | 80 | 98 | 87 | 4 | 4 | 0 | 8 | 1.71 | 1.82 | 0.00 | 1.27 |
| Giraffe | 15 | 18 | 17 | 18 | 18 | 0 | 2 | 0 | 2 | 0.00 | 4.28 | 0.00 | 1.53 |
| Red Hartebeest | 140 | 132 | 145 | 131 | 136 | 6 | 5 | 5 | 16 | 1.64 | 1.25 | 2.18 | 1.63 |
| Kudu | 750 | 800 | 800 | 900 | 833 | 33 | 42 | 31 | 106 | 1.49 | 1.91 | 1.97 | 1.76 |
| Eland | 115 | 105 | 110 | 93 | 103 | 8 | 8 | 3 | 19 | 2.74 | 2.64 | 1.84 | 2.55 |
| Gemsbok | 55 | 61 | 61 | 54 | 59 | 3 | 3 | 1 | 7 | 1.77 | 1.79 | 1.06 | 1.65 |
| Warthog | 25 | 65 | 75 | 184 | 108 | 3 | 19 | 16 | 38 | 1.66 | 9.21 | 4.97 | 4.86 |
| Ostrich | 55 | 42 | 41 | 21 | 35 | 12 | 2 | 1 | 15 | 10.29 | 1.77 | 2.72 | 5.98 |
| Wildebeest (black) | 165 | 92 | 128 | 72 | 97 | 24 | 6 | 13 | 43 | 9.39 | 1.70 | 10.32 | 6.10 |
| Springbok (black) | 10 | 7 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 5.14 | 0.00 | 0.00 | 5.92 |
| Wildebeest (blue) | 9 | 3 | 2 | 1 | 2 | 2 | 2 | 0 | 4 | 24.00 | 36.35 | 0.00 | 27.63 |
| TOTAL | 4491 | 4680 | 4834 | 5032 | 4849 | 130 | 133 | 88 | 351 | 3.53 | 3.63 | 1.00 | 1.00 |

Table 2. The preference indices for species killed by lions on Shamwari for each year of the study period and the overall preference indices calculated from the subset of data.

| | COUNTS | | | | KILLS | | | | PREFERENCES | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Year 1** | **Year 2** | **Year 3** | **Overall** | **Year 1** | **Year 2** | **Year 3** | **Overall** | **Year 1** | **Year 2** | **Year 3** | **Overall** |
| Mountain reedbuck | 300 | 350 | 350 | 333 | 1 | 0 | 0 | 1 | 0.18 | 0.00 | 0.00 | 0.06 |
| Impala | 694 | 600 | 852 | 715 | 1 | 1 | 1 | 3 | 0.08 | 0.09 | 0.13 | 0.09 |
| Duiker | 900 | 900 | 850 | 883 | 1 | 7 | 2 | 10 | 0.06 | 0.40 | 0.27 | 0.24 |
| Springbuck | 257 | 220 | 153 | 210 | 0 | 2 | 1 | 3 | 0.00 | 0.47 | 0.75 | 0.31 |
| Bushbuck | 750 | 900 | 950 | 867 | 6 | 10 | 2 | 18 | 0.42 | 0.57 | 0.24 | 0.44 |
| Zebra | 84 | 80 | 98 | 87 | 2 | 3 | 0 | 5 | 1.25 | 1.93 | 0.00 | 1.22 |
| Blesbuck | 305 | 340 | 243 | 296 | 12 | 5 | 1 | 18 | 2.07 | 0.76 | 0.47 | 1.30 |
| Waterbuck | 65 | 65 | 62 | 64 | 1 | 0 | 3 | 4 | 0.81 | 0.00 | 5.53 | 1.33 |
| Gemsbok | 61 | 61 | 54 | 59 | 1 | 2 | 1 | 4 | 0.86 | 1.69 | 2.12 | 1.46 |
| Kudu | 800 | 800 | 900 | 833 | 25 | 30 | 18 | 73 | 1.64 | 1.93 | 2.29 | 1.87 |
| Red hartebeest | 132 | 145 | 131 | 136 | 4 | 5 | 5 | 14 | 1.59 | 1.77 | 4.37 | 2.20 |
| Eland | 105 | 110 | 93 | 103 | 6 | 5 | 0 | 11 | 3.00 | 2.34 | 0.00 | 2.29 |
| Giraffe | 18 | 17 | 18 | 18 | 0 | 2 | 0 | 2 | 0.00 | 6.05 | 0.00 | 2.42 |
| Warthog | 65 | 75 | 184 | 108 | 2 | 15 | 5 | 22 | 1.62 | 10.29 | 3.11 | 4.35 |
| Wildebeest | 92 | 128 | 72 | 97 | 17 | 4 | 4 | 25 | 9.72 | 1.61 | 6.35 | 5.49 |
| Ostrich | 42 | 41 | 21 | 35 | 8 | 2 | 1 | 11 | 10.02 | 2.51 | 5.45 | 6.78 |
| Springbuck (black) | 7 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 7.51 | - | - | 9.15 |
| Wildebeest (blue) | 3 | 2 | 1 | 2 | 1 | 1 | 0 | 2 | 17.53 | 25.71 | 0.00 | 21.36 |
| Total | 4680 | 4834 | 5032 | 4849 | 89 | 94 | 44 | 227 | 3.24 | 3.42 | 1.83 | 3.46 |

# APPENDIX D

## Home range sizes from previous studies of lion biology

| Range size | Location | Source | Comments |
|---|---|---|---|
| Very large | Serengeti | Hanby *et al.* 1995 in Hunter 1998 | Food supplies ephemeral and dens sites widely scattered |
| Small | Ngorongoro Crater | Hanby *et al.* 1995 in Hunter 1998 | Density of food and den sites greater and more evenly distributed |
| 2075 km$^2$ | Etosha | Stander 1991 | Ungulates migratory and at low density |
| 87.5 km$^2$ | Ngorongoro Crater | Elliot & McTaggart Cowan 1978 | |
| 121.4 km$^2$* | East Africa | Woodroffe & Ginsberg 1998 | |
| 52.83±35.68 km$^2$ | Phinda | Hunter 1998 | |
| 42-369 km$^2$ | Chobe | Viljoen 1993 | Dry-season ranges were on average 1.7 times larger than wet season ranges |
| 1178 & 1745 km$^2$ (prides); 243-5415 km$^2$ (nomadic males) | North-eastern Namibia | Stander 1997 | |

* an average taken from 59 studies