THE BEHAVIOURAL ECOLOGY OF A SOLITARY LION PRIDE IN KARONGWE GAME RESERVE

by

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DECLARATION BY CANDIDATE

I hereby declare that the dissertation submitted for the degree, M Tech: Nature Conservation, at Tshwane University of Technology is my own original work and has not previously been submitted to any other institution. I testify that that all authors quoted are indicated and acknowledged by means of a comprehensive list of references. The financial assistance of Tshwane University of Technology towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the Tshwane University of Technology.

Monika Brigitte Lehmann
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ABSTRACT

The increasing number of small reserves reintroducing lions (*Panthera leo*) calls for a greater knowledge base of how lions behave in such small areas. For lions to be managed effectively on small reserves their territorial, reproductive and feeding behaviour needs to be understood. A single pride of lions on the Karongwe Game Reserve was studied for six years after their release onto the reserve, from 1999-2005. Over this period the pride consisted of between four and eleven lions. Their home range was larger in summer, and water was found to be important to the placement of these territories. Male lions were found to respond to resource limitations and not social factors for the utilisation of the home range, but did respond to social factors when on territorial patrol. Female lions were also shown to respond to resource factors, but had a stronger response to the social effect of a neighbouring pride. Mating behaviour of the pride was similar to that shown in larger reserves, but the lack of conspecific competition resulted in altered parameters such as increased birth rate and reduced inter-birth interval, resulting in a higher growth rate when compared with the Kruger National Park, but similar to other small reserves in South Africa. The feeding behaviour of the lions was studied, with a particular focus on the number of kills made by different lion groups. Although there was preference for some species, there was no significant selection for prey size, age and gender. A two male coalition or dispersing subadults increased the number of kills made. The single male shared a large number of kills with the pride. Lions can potentially have a substantial impact in small reserves, and it is thus important to understand their biology in order to manage the appropriate driving factors effectively.

EKSERP

Die stygende aantal klein reservate waarin leeus (*Panthera leo*) hervestig word, vereis meer kennis oor hul gedrag in sodanige areas. Om die effektiewe bestuur van die spesie in klein reservate te verseker, moet hul territoriale, reproduktiewe en voedingsgedrag verstaan word. ‘n Enkele trop leeus is vir ses jaar in die Karongwe Wildreservaat bestudeer na hul vrylating in 1999. In hierdie tydperk het die trop bestaan uit vier tot elf leeus. Hulle territorium was groter in die somer en water het ‘n belangrike rol gespeel in die ligging van territoriums. Die trop se paringsgedrag was soortgelyk aan dié gedokumenteer in groter reservate, maar die afwesigheid van kompetisie met ander groepe van dieselfde spesie het ‘n verandering in parameters veroorsaak. Die aanwastempo was gevolglik hoër as in die Kruger Wildtuin, maar soortgelyk aan ander klein reservate in Suid-Afrika. Alhoewel daar ‘n voorkeur vir sekere prooi-spesies was, was daar geen noemenswaardige voorkeur ten opsigte van grootte, ouderdom of geslag nie. ‘n Koalisie tussen twee mannetjies of ‘n sub-volwasse verspreidingsgroep het die getal vangste verhoog. Leeus kan ‘n substansiële impak op klein reservate hê, daarom is dit belangrik om hul biologiese gedrag te verstaan ten einde die toepaslike drywers doeltreffend te bestuur.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 THE NEED FOR STUDIES ON SMALL RESERVES

Over the past few decades human development has caused a decrease in large, natural areas (Orford, Perrin & Berry 1988; Stander 1991). As these large areas are rapidly decreasing, conservationists and reserve managers have increasingly turned towards small (<1000 km^2), enclosed reserves to re-establish species to their former state. As this primarily serves as a tourist attraction, it involves reintroducing megafauna, including large predators, onto relatively small reserves (Hunter *et al.* in press). Such small reserves, however, are usually enclosed, creating problems managers need to address. This is because fences restrict the immigration and emigration of animals and unless these small reserves are monitored and managed effectively, isolation could have a negative effect on genetics, social structure and the delicate balance between predator and prey populations.

Lions (*Panthera leo*) have been studied in detail in large open systems such as the Serengeti and the Kruger National Park by authors such as Schaller (1972), Van Orsdol, Hanby & Bygott (1985), Packer *et al.* (1988) and Funston *et al.* (1998). Relatively little, however, has been published on the behaviour and management of reintroduced lions in small reserves.

1.2 BACKGROUND

Lions are large, social carnivores that live in prides, which are permanent social units that may exist for many generations (Schaller 1972; Van Orsdol *et al.* 1985; Packer, Scheel &

Pusey 1990). Although the pride is a cohesive social unit its members may be scattered in several groups throughout the pride's range at any one time (Van Orsdol *et al.* 1985), and it is rare to find all pride members together (Packer 1986). Related or unrelated males bond together to form a coalition to increase their chance of tenure in a pride (Bygott, Bertram & Hanby 1979). It was previously believed that lions formed groups to increase hunting success but it is now believed that prides are formed for co-operative cub defence and group territoriality (Packer *et al.* 1990).

There is a considerable amount of literature on the territorial behaviour of lions, although this aspect seems to have been less the focus than other aspects such as social structure, breeding and feeding ecology. A territory is an area which satisfies an animal's energetic needs and is defended by the resident (Henschel & Skinner 1991). It is thought that a carnivore may favour ranges that are as large as necessary but as small as possible (MacDonald 1983). Seasonal variation in home range size occurs (Viljoen 1993), and due to seasonal variation in prey availability, it would be expected that home range sizes change (Van Orsdol *et al.* 1985). Territories also serve indirectly to protect cubs (Funston *et al.* 1998). Males maintain a territory and discourage rivals from entering it by patrolling, scent-marking and roaring (Bertram 1973; Van Orsdol *et al.* 1985; Funston *et al.* 1998). Studies show that females can distinguish immediately between roars from their pride males and unfamiliar males (McComb *et al.* 1993; Pusey & Packer 1994), and that they become agitated and retreat with their cubs when they hear unfamiliar calls. Territorial behaviour is an important factor in lion social behaviour and is vital for the protection and survival of cubs.

The mating behaviour of lions has been the topic of several papers. A male's reproductive lifespan is limited to the period in which he has tenure (Van Orsdol *et al.* 1985) which can last anything from 18 months to 90 months, with an average of 38 months (Packer *et al.* 1988). Females in a pride tend to come into oestrus together and give birth synchronously (Bertram 1975a). They typically have their first litter at three to four years (Packer *et al.* 1988) and have a mean of two to three cubs (Van Orsdol *et al.* 1985). The average interbirth interval is 24 months (Bertram 1975a; Packer & Pusey 1987).

Feeding behaviour of lions has been studied in depth. Stander (1991) states that although it was originally believed that females do most of the hunting, (Schaller 1972; Scheel & Packer 1991), males may hunt on their own. Funston *et al.* (1998) found that in Kruger National Park, male lions acquire most of their food by hunting rather than scavenging, although they still hunt significantly less frequently than females.

All of the above studies were conducted in large open systems. The information is no doubt valuable to managers in small reserves, but certain behaviour may be different in small reserves. Lions also need to be more intensively managed in such reserves to prevent the depletion of the prey base in the area (Peel & Montagu 1999; Power 2002a; Druce *et al.* 2002a) and to control population growth. There is relatively little literature available on how to manage reintroduced populations of predators (Funston & Jolley in prep.). Knowing what a species' home range size is, along with prey abundance, can provide managers with important information with regards to reserve size and the number of individuals it can sustain. Habitat use can provide information on the importance of certain features in the landscape to the species. Reproductive parameters need to be understood by managers so that population growth can be predicted and controlled effectively. The feeding requirements of a pride are particularly important to determine how many lions the reserve can sustain, and which species are most likely to be preyed upon.

1.3 OBJECTIVES OF THIS STUDY

The specific objectives of the study are to compare behavioural ecology of a reintroduced pride with published information from larger reserves, particularly Kruger National Park. The dissertation has been written in the format of three papers for submission to scientific journals, and each chapter therefore has its own methods, objectives, as well as results and discussion.

The territorial chapter aims to: (1) describe home range utilisation by the lions, and to determine whether lions respond to resource or social factors in their distribution; (2) calculate the home range size required by the different lion sub-groups; (3) determine seasonal differences and the importance of water to the placement of territories; and (4) study the territorial behaviour of the single male.

The objectives of the reproductive chapter are to: (1) describe the reproductive parameters of lions living without conspecific competition.

The feeding chapter's objectives are to: (1) describe the diet of lion on a small reserve including prey selection and biomass removal; (2) assess the impact of one-male versus two-male coalition on ungulate prey; and (3) assess the impact of dispersing sub-adult males on ungulate prey.

Management recommendations are provided for manipulation of population size and pride composition based on the results.

The study aims to contribute to the knowledge base of the specific requirements and behaviours of reintroduced populations, in order to manage the species with greater understanding in these small, enclosed reserves.

CHAPTER 2

METHODS

2.1 STUDY AREA

Fieldwork was conducted on Karongwe Game Reserve, located in the Limpopo Province, South Africa. Karongwe is an 85 km^2 conservancy that was formed in 1998. It lies roughly halfway between Tzaneen and Hoedspruit, with the centre of the reserve at 24^{o}13'S and 30^{o}36'E (Figure 2.1). The Greater Makalali Conservancy borders Karongwe on its eastern boundary and is the only other reserve in the area that supports lions (Figure 2.2).

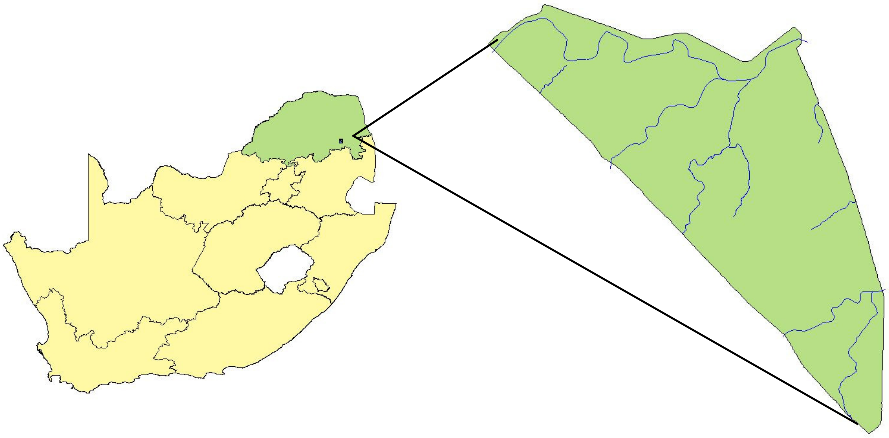


Figure 2.1. Location of Karongwe Game Reserve in Limpopo Province, South Africa

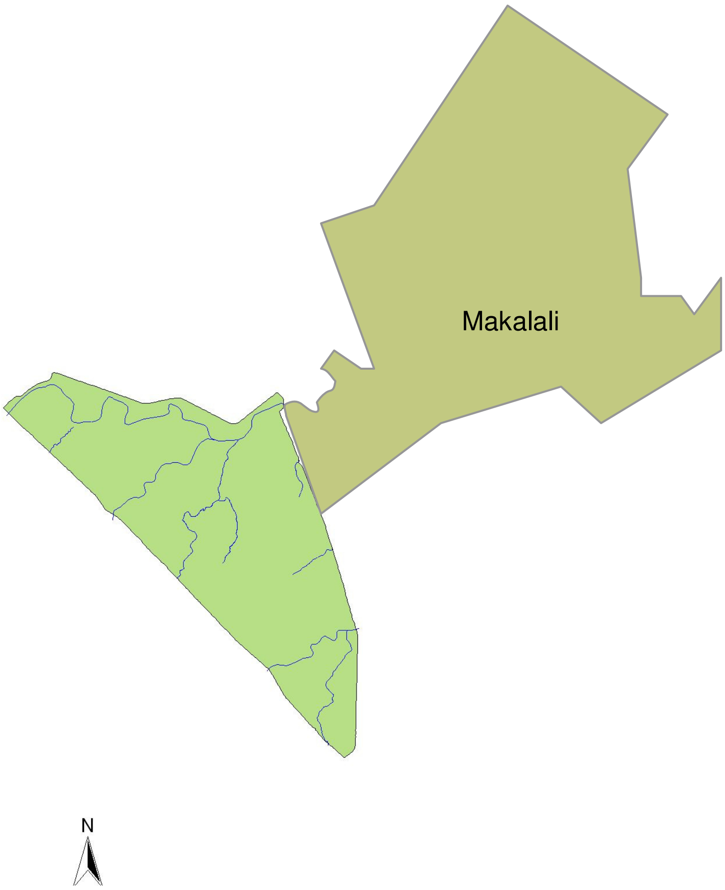


Figure 2.2. Location of Makalali Game Reserve in relation to Karongwe Game Reserve

2.1.1 Topography

Altitude varies from 520 m above sea level in the west to 489 m above sea level in the east. Several, both large and small, koppies (rocky outcrops) are scattered around the reserve. A large number of drainage lines, predominantly flowing from west to east, form part of the topography. The Makhutswi River in the north is the only perennial river. The Kuvyenami and Mafunyane Rivers drain the central part of the reserve, and the Korongwe and Mathumi Rivers drain the south (Figure 2.1). All the rivers eventually join up with the Olifants River.

2.1.2 Geology and soils

Basement gneisses and granites underlie the Lowveld region, with numerous dolerite intrusions and areas covered by gabbro (Low & Rebelo 1998). According to the geological map of the area, the Makhutswi gneiss complex that consists of biotite gneiss dominates the northern and northwestern parts of the reserve. The southern and central areas are interspersed with coarse-grained, quartz-rich biotite-muscovite granite of the Harmony Granite (Walraven 1989). The substrate is characterised by sandy soils in the uplands and clayey soils with high sodium content in the bottomlands (Low & Rebelo 1998).

2.1.3 Climate

Temperatures range from 0°C to 45°C, with an average of 22°C. Karongwe Game Reserve falls within a summer-rainfall area. Rain falls mainly between October and April, with December to February being the wettest months. Average rainfall for the past 14 years is 478 mm.

2.1.4 Vegetation type

The reserve falls within the Savanna Biome (Rutherford & Westfall 2003) and lies within the Mixed Lowveld Bushveld (Low & Rebelo 1998). The vegetation can be described as having dense bush on the uplands, open tree savanna in the bottomlands, and dense riverine woodland on the riverbanks. The shrub layer is moderately developed and the grass layer is poorly to moderately developed (Low & Rebelo 1998). It is characteristic *Acacia nigrescens – Sclerocarya – Digitaria* savanna. *Acacia spp* and *Combretum spp* are important, and there is evidence of *Colophospermum mopane* in the area as it is near the transition with Mopane Bushveld.

2.1.5 Fauna

As the reserve's main function is eco-tourism a large number of species are present. Apart from lions, other large carnivores include leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*) and spotted hyeanas (*Crocuta crocuta*), and there are twelve ungulate species that support them.

2.1.6 Lion population

The study was conducted over a six year period from October 1999 to October 2005, totalling 2192 field days. During that time the lion population size varied from four to a maximum of eleven lions, with an average of eight, and eleven lions were removed to control population size. The founder population consisted of a coalition of two brothers and two unrelated sisters. After three years, on 14 June 2002, one of the males was removed from the coalition as the pair was considered to be removing more and larger prey than a single male would, and a single male would suffice for ecotourism. Over the six-year period the lions had six litters consisting of either two or three cubs. The first cubs reached subadult age in 2002, and consisted of one male and one female. Thereafter a subadult group was present each year. All subadult lions were removed from the reserve between the ages of 17 and 36 months (n = 11).

2.2 FIELD DATA COLLECTION

A member of each subgroup of the population (male coalition, pride females and subadult group) was radio-tracked twice daily where possible for the duration of the study (92.3% of days, n = 2024), using the standard method for radio telemetry tracking (Mills 1996).

The lions were tracked using telemetry until visual was obtained, or if that was not possible due to their location in thick vegetation, to get as close to the lion's location as possible. Most observations took place between 5:00-10:30 (48.4%, n = 1809) and 15:30-20:30 (47.7%, n = 1782), with some observations at night (3.9%, n = 147). The nocturnal observations will be discussed in greater detail in Chapter 3.

After locating the focal animal, the following data were recorded: date, time, location, GPS co-ordinate, daily belly score, and general behaviour. Any behaviour relating to reproductive biology was recorded. All found kills were recorded. More details on methods regarding reproductive and feeding behaviour are discussed in Chapters 4 and 5 respectively.

Data was collected by several researchers. K.e.r.i. Research headed by Cailey Owen was the primary organisation in control of data collection and storage, and over the study period employed five people to collect field data. This organisation was assisted by Global Vision International (GVI) who employed several staff members over the six years to assist in data collection. Daily field data was therefore collected by several people, all of which were trained by Cailey Owen to collect data in a standardised and accurate manner. The author was employed by K.e.r.i. research for three years. During that time the author assisted in collecting daily field data and was the only person to collect the nocturnal data used in the territorial chapter. All data assimilation and analyses were done by the author.

Another study to be undertaken by K.e.r.i. Research in the future will show the offtake by all large predators and intraguild behaviour and was therefore not included in this study.

2.3 DATA ANALYSIS

Data were analysed differently in each chapter. Statistical tests used were similar throughout and include chi-square tests to analyse frequencies, determine goodness of fit or to test for association. All other data were analysed using one-way analysis of variance (ANOVA). In the territorial chapter a grid of 1 km x 1 km was placed over the reserve map and a frequency of roaring and scent marking in each grid cell was determined. The grid was also used to determine preference values for grid cells across the reserve. This was done to contrast the social versus resource inputs. Grid use was calculated as the proportion of all location points that fell in each grid cell. Grid preference was then calculated as the ratio of use to availability (Spong 2002), where a value of one indicated the area was utilised at its availability, >1 indicated a preference and <1 indicated avoidance of an area.

CHAPTER 3

TERRITORIAL BEHAVIOUR

3.1 INTRODUCTION

Knowing a species' home range size can provide managers with important information with regards to reserve size and the number of individuals it can sustain. Habitat use can provide information on the importance of certain features in the landscape to the species.

Factors such as energy expenditure in defending the area may set the upper limits of territory size (Bertram 1973) while lower limits are set according to food availability (Van Orsdol *et al.* 1985). Animals defend their territories from conspecifics (Henschel & Skinner 1991). This is done by displaying certain territorial behaviour. Male lions patrol by visibly walking with a proud posture in an open, unconcerned manner (Funston, Mills & Richardson in prep.). Scent-marking is usually done by the male, either by rubbing the head on the branches and then squirting urine upwards into the bush; or by squirting downwards onto the ground and rubbing the hind feet in it (Schenkel 1966; Funston, Mills & Richardson in prep.). Chemical odours placed so that their chances of discovery by conspecifics are maximised is a form of olfactory communication in carnivores (Gorman & Trowbridge 1989). Roaring is often a territorial display in which the whole pride is involved (Schenkel 1966), although males often leave the pride behind when on territorial patrol (Funston 1999).

Territorial displays are expensive because (1) they separate the males from their females, increasing the risk of infanticide by invading males (Packer & Pusey 1983a; Packer

2000), and (2) because they highlight the location of the males for any intruding coalitions (Packer & Pusey 1997; Grinnell & McComb 2001). They are also energetically expensive, both in terms of the distances covered (Bertram 1973), and the energetic cost of roaring (Funston 1999). Territory sizes and boundaries are influenced by the resource base of the area (Ogutu & Dublin 2004; Packer *et al.* 2005), and will increase or decrease depending on available resources (Van Orsdol *et al.* 1985).

The two factors of advertisement and resources may influence territory and home range size, shape, and usage in different ways (Starfield, Furniss & Smuts 1981; Spong 2002). It is extremely difficult to separate these two potentially confounding factors in natural circumstances. However, there was an opportunity to test their relative influences in an artificial situation where a single pride male and pair of females existed in a fenced reserve, and a second pride and males were in a fenced area to one side of them. It was thus possible to separate the predictions from advertisement and resources, and assess their relative input to lion behavioural decisions and subsequent costs.

It was predicted that lions would respond towards resources equally in all directions, but would respond to social influences only in the direction of the adjacent pride. Male and female range use was measured, as well as male scent-marking and roaring in different parts of their range. The relative influence that the social factors impose on the resource factors was assessed.

3.2 METHODS

The nocturnal observations used for the territorial study did not span over the whole study period. The research organisation on the reserve (K.e.r.i. Research) was involved in regular nocturnal intraguild research twice weekly during 2004. These observations took place from 22h00 to 02h00, and locations of all predators including the lions were recorded. A separate nocturnal study was undertaken to focus more specifically on lion territorial behaviour from February 2005 to June 2005. Forty-eight nights were spent with the pride male as the focal animal and whichever pride members were with him. To provide repeatability the 48 nights were divided into twelve sessions of four consecutive nights each. Three shift times were chosen: 17:00-23:00, 21:00-04:00, and 23:00-06:00. These times were chosen as they incorporate dusk, the middle of the night, and dawn. One session for each shift time in each of the four moon phases was completed. Four nights were spent following the lions continuously from 17:00-06:00.

The male was followed by vehicle at a distance of 15-30 m. Lions were viewed using a spotlight with a red filter to reduce any negative effect the bright light could have on their eyes. Any territorial behaviour activities were recorded. This included roaring, scent-marking and information about whether the animal was moving or stationary. A GPS location was recorded at every change in direction and at every location where the animal scent marked or roared.

3.2.1 Data analysis

The data were imported into Arcview 3.2 where home range analyses and animal movement paths were created using the extension package Animal Movement analysis (Hooge 1999). Minimum convex polygons were created as they are the simplest and one of the most widely used methods for constructing home ranges (Creel & Creel 2002; Getz & Wilmers 2004). Kernel home ranges were also created for a more descriptive image as they are very useful for determining the utilisation distribution and density of a population (Worton 1989). When creating kernel home ranges 95% was used to denote the range as this includes most locations visited by the lions except the few that lie outside their usual territory (Burt 1943; Seaman & Powell 1996; Apps 1999), and fifty percent was chosen to denote the core area as in other studies (Mizutani & Jewell 1998). A grid of 1 km x 1 km was placed over the reserve map and a frequency of roaring and scent marking in each grid cell was determined. The grid was also used to determine preference values for grid cells across the reserve. This was done to contrast the social versus resource inputs. Grid use was calculated as the proportion of all location points that fell in each grid cell. Grid preference was then calculated as the ratio of use to availability (Spong 2002), where a value of one indicated the area was utilised at its availability, >1 indicated a preference and <1 indicated avoidance of an area. A buffer of 2 km was created along the eastern boundary closest to the neighbouring pride. This distance was chosen because Funston (1999) found that lions responded to roars within 2 km but generally not if the other lions were further away. It could be assumed that this distance of 0-2 km was the zone in which lions respond to neighbouring lions, and was used in this study to determine the social response. Whether the buffer zone was preferred or avoided indicated the lions' social response to the other reserve's pride. Resource limitation and preference was measured on one scale by contrasting observed ranges with available ranges, and also assessing the influence of rivers. This was done by determining the preference for areas within 500 m of drainage lines. The data created from Arcview 3.2 were transferred into a spreadsheet for assimilation and statistical analyses. A habitat or vegetation map would have been useful for home range analysis but unfortunately no such map of the reserve exists to this date and could not be used in the analysis.

3.3 RESULTS

3.3.1 Home range expansion

Two male lions were released onto the reserve in September 1999, and two lionesses were released a month later. The range available to the lions was 80 km^2. The lion's 95% home range for the first year was 35.0 km^2 and their 50% core range was only 1.2 km^2 in size. Over the years the lion home range has expanded to 65.4 km^2 with a core of 5.5 km^2 (Table 3.1). The minimum convex polygon expanded from 76.9 in 2000 to 77.9 in 2005.

Table 3.1. Combined male and female annual minimum convex polygon and kernel home range sizes, illustrating the expansion of the home range from 2000 to 2005

Home Range	95% range (km^2)	50% core (km^2)	Minimum convex polygon (km^2) *
2000	35.0	1.2	76.9
2001	59.5	5.7	78.1
2002	63.5	7.2	74.7
2003	52.4	4.3	72.9
2004	59.7	5.5	73.6
2005	65.4	5.5	77.9
Management action (splitting male coalition)			
Before	68.8	6.3	78.6
After	66.0	5.1	78.1

* Area of clipped minimum convex polygon that falls within the reserve boundary

3.3.2 Home range utilisation

Figure 3.1 clearly shows how the lion core home range was along the rivers. The pride's home range (95% range 64.4 km^2 and 50% core 10.3 km^2) was larger than the males' home range (95% range 56.3 km^2 and 50% core 5.0 km^2) with the core double the size of that of the males. The subadult males had a 95% range similar to the females (66.3 km^2)

Figure 3.1. Lion home range in the first year after reintroduction (2000) and last year of the study (2005)

while their core was more like that of the males (5.6 km^2). There was a noticeable difference between the summer home range (November – April) and the area utilised in winter (May – October). The lions utilised almost the whole reserve in summer (95% range 77.4 km^2 and 50% core 10.6 km^2) with a large core encompassing a larger area away from the rivers. The winter home range had a 95% range of 58.9 km^2 and a 50% core of 6.1 km^2. Almost 70% of the reserve lies within 500 m of generally permanent water with 58.2% of the summer home range, and 86.8% of its core lay within 500 m of water, while 99.1% of the winter core range was within this area.

The size of the home range used by all the lions since the removal of a pride male was not significantly different from the size of the home range before ($\chi^2_1 = 0.074$, NS) (Table 3.1). The pride's home range expanded from 53.4 km^2 to 56.8 km^2 which was not significant ($\chi^2_1 = 0.286$, NS), although the spatial utilisation changed.

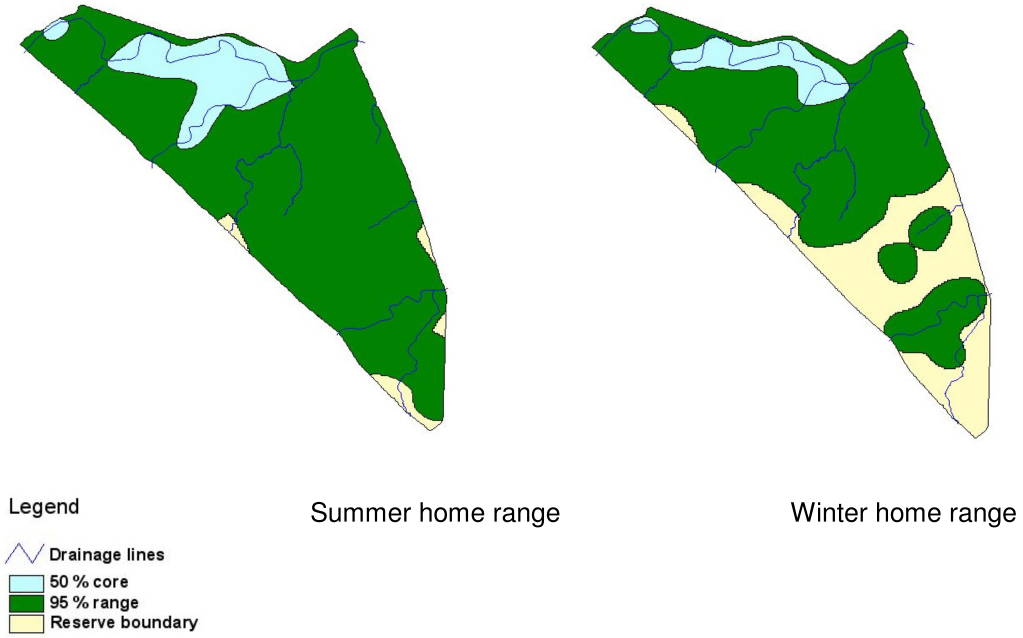
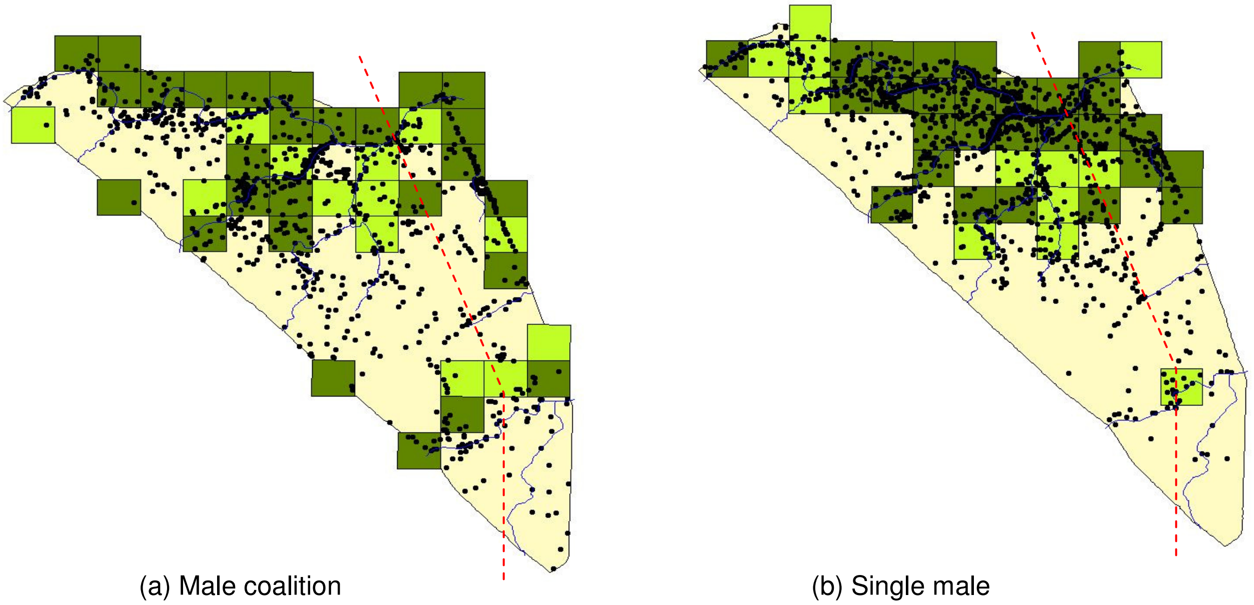


Figure 3.2. Lion home range in summer and winter over the duration of the study period

Before the male was removed the lionesses spent little or no time in the eastern side of the reserve, but have included that area since then. While the coalition was present they had a home range of 66.6 km^2 and a core of 6.2 km^2 that was reduced to 47.4 km^2 with a core of 4.8 km^2 when the male was removed. This was, however, not a significant difference ($\chi^2_1 = 0.018$, NS), even though the size of the home range was almost 20 km^2 smaller.

3.3.3 Response to resource and social factors

Each 1 km x 1 km grid cell on the reserve was tested for preference (Figure 3.2). All lion groups selectively avoided more than half of the reserve (Table 3.2). Between 50-62% of the buffer zone along the eastern boundary was avoided by the males and subadults, although the buffer zone was utilised at just above availability (p = 1.08 – 1.18). The female lions, however, avoided 87.5% of the buffer zone and therefore tended to avoid it (preference index = 0.56).



(a) Male coalition

(b) Single male

(c) Females

(d) Subadult males

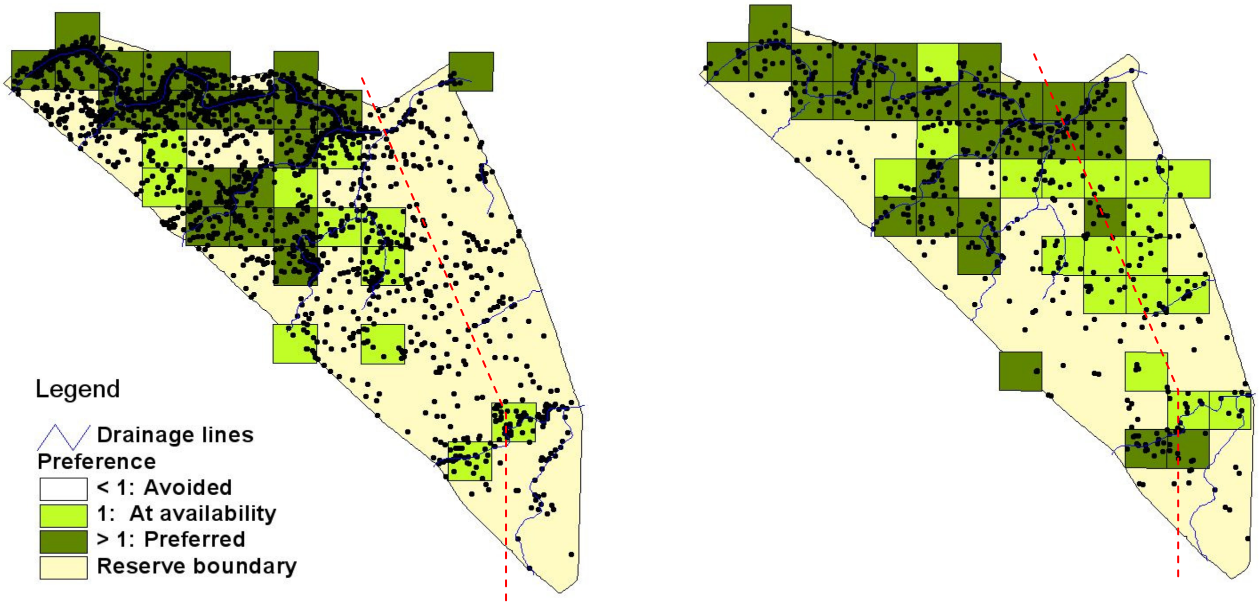


Figure 3.3. Maps of (a) male coalition, (b) single male, (c) females and (d) subadult males, indicating areas of the reserve that are preferred, avoided or utilised according to availability. The red line indicates the edge of the 2 km buffer zone.

When taking grid use into account there was no apparent difference between the coalition and single male's preference for certain areas (Figure 3.2). The coalition preferred cells scattered around the reserve and therefore spent more time in those areas than the single male did. The single male preferred areas mostly in the northern half of the reserve, which coincided with the female's preference, and was also along the major drainage lines. The subadults used the largest proportion of the buffer and also had a more random distribution of preferred cells across the reserve. The area within 500 m of drainage lines was preferred by all lion groups (preference index = 1.02-1.13) according to its availability, with the females showing the highest preference.

Table 3.2. The percentage of the reserve that is preferred, avoided, or used at availability by the different lion groups measured (a) across the whole reserve, and (b) within the 2 km buffer zone along the eastern boundary to indicate the response to social factors

Preference (use/availability)	**Females (%)**	**Male coalition (%)**	**Single male (%)**	**Subadult males (%)**
Over the whole reserve				
Preference (>1)	23.5	29.4	26.5	27.5
At Availability (1)	11.8	13.7	11.8	17.6
Avoidance (<1)	64.7	56.9	61.8	54.9
Within the 2 km buffer zone along eastern boundary				
Preference (>1)	3.1	25.1	28.1	18.7
At Availability (1)	9.4	18.8	9.4	31.3
Avoidance (<1)	87.5	56.1	62.5	50.0

3.3.4 Movement patterns

The pride male walked an average of 446 ± 72.79 m/hour on the nights he was followed ($n = 48$). Figure 3.3 shows movement paths walked on selected nights when more than 4 km were covered. The largest distance covered in one six hour observation was 12.0 km and took place between 21:00 and 04:00 on a clear night with the moon in its first quarter. On nine nights the pride male and any associated lions with him did not walk at all. The lions had a kill on three of those and the male was mating on two of the others.

The distances he moved did not seem to be affected by cloud cover (ANOVA, $F_{2,45} = 0.963$, $p = 0.389$), time of night (17:00 – 00:00; 21:00 – 04:00; or 23:00 – 06:00) (ANOVA, $F_{2,45} = 1.014$, $p = 0.370$), or the phase of the moon (ANOVA, $F_{3,44} = 2.306$, $p = 0.089$) (SE = 436.76). However, when the time of night and the moon phase were combined they were highly significant ($n = 48$, $\chi^2_6 = 7791.4$, $p < 0.01$), with the furthest distance being walked on full moon between 21:00 – 04:00 (mean 6.4 km, $n = 4$), and the shortest distances being walked on new moon between 17:00 – 00:00 (mean 0.3 km, $n = 4$). The male walked less than expected between 23:00 – 06:00 during all four moon phases, and more than expected between 21:00 – 04:00 during both full moon and the first quarter.

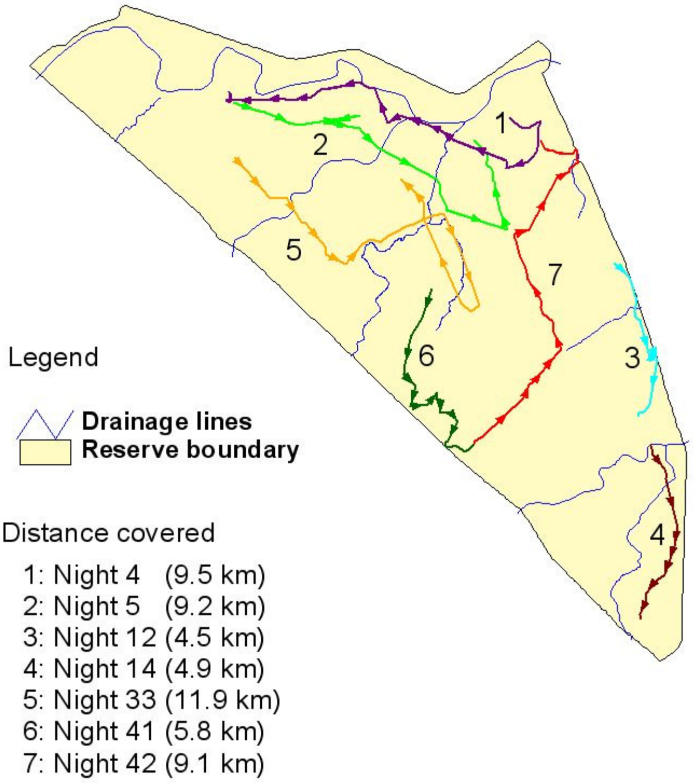


Figure 3.4. Selected nights showing movement paths travelled by the pride male, illustrating distance and path walked during territorial patrols

3.3.5 Territorial behaviour

The pride male covered significantly more distance while on his own than when other members of the pride were with him (ANOVA, $F_{1,46} = 11.606$, $p < 0.001$). Overall 627 scent marks were observed by all lions in the reserve, as compared with only 194 excretions. Additionally the lions were heard roaring 761 times (Table 3.3), and 74.3% (n = 1313) of all territorial scent marks and roars occurred within drainage lines or within 500 m of water.

Table 3.3. A comparison between territorial behaviour and excretions for each lion group in each observation period

Observation period	Days	Scent marks	Roars	Urinate / defecate
Before management action				
Male	988	126	55	33
Female	988	2	24	20
	Total	**128**	**79**	**53**
After management action				
Male	1130	328	352	58
Female	1130	0	80	28
Subadults	1130	1	14	8
	Total	**329**	**446**	**94**
Nocturnal observation after management action				
Male	48	170	171	28
Female	48	0	62	18
Subadults	48	0	3	1
	Total	**170**	**236**	**47**

The coalition was found to show a preference (preference index = 1.24) for scent marking within the buffer zone along the eastern boundary. The single male showed a weaker preference (preference index = 1.03) while the rest of the reserve was utilised by both the coalition and single male at just below availability. In terms of roaring, the coalition showed a strong preference for utilising the buffer zone (preference index = 1.53) and the single male utilised it at just below availability (preference index = 0.87). The coalition utilised the rest of the reserve below availability and the single male utilised it at availability.

3.3.6 Scent marking by the pride male

The single pride male scent marked at a rate of 1.1 scent marks/km (SE = 0.5). These included rubbing the body or head on bushes (21.7%), spray urinating (41.4%), and urinating onto the ground while scraping with the back feet (36.8%). Whether the male was alone or with members of the pride did not affect the rate of scent marking (ANOVA, $F_{1,46} = 0.174$, $p = 0.678$, SE = 0.515). Most scent marking took place in the northern and eastern sections of the reserve. Figure 3.4 indicates the locations of scent marks made by the male(s) before and after the management action.

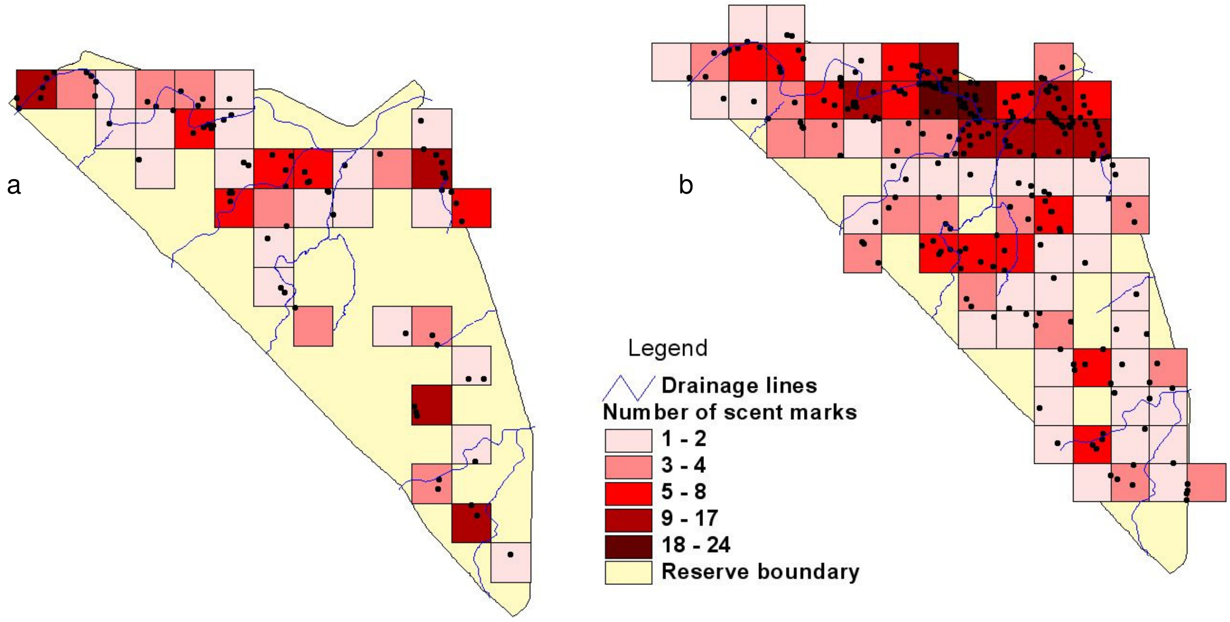


Figure 3.5. Locations of scent marks made (a) by the pride males from 1999 to 2002 and (b) by the single male from 2002-2005, indicating the density of scent marks across the reserve

3.3.7 Territorial roaring by the pride male

The single pride male roared at a rate of 0.6 roars/hour (SE = 0.76, n = 48). The male roared significantly more frequently while alone (ANOVA, $F_{1,46} = 14.522$, $p < 0.001$, SE

= 0.798) than with pride members, with an average of 2.0 roars/hour while alone compared to 0.4 roars/hour when not alone. Figure 3.5 indicates the location of roars by the coalition and the single male.

All movement and most territorial data were unfortunately only collected after the removal of one male. Therefore any sound comparisons between the one male and a two male coalition's behaviour was not possible.

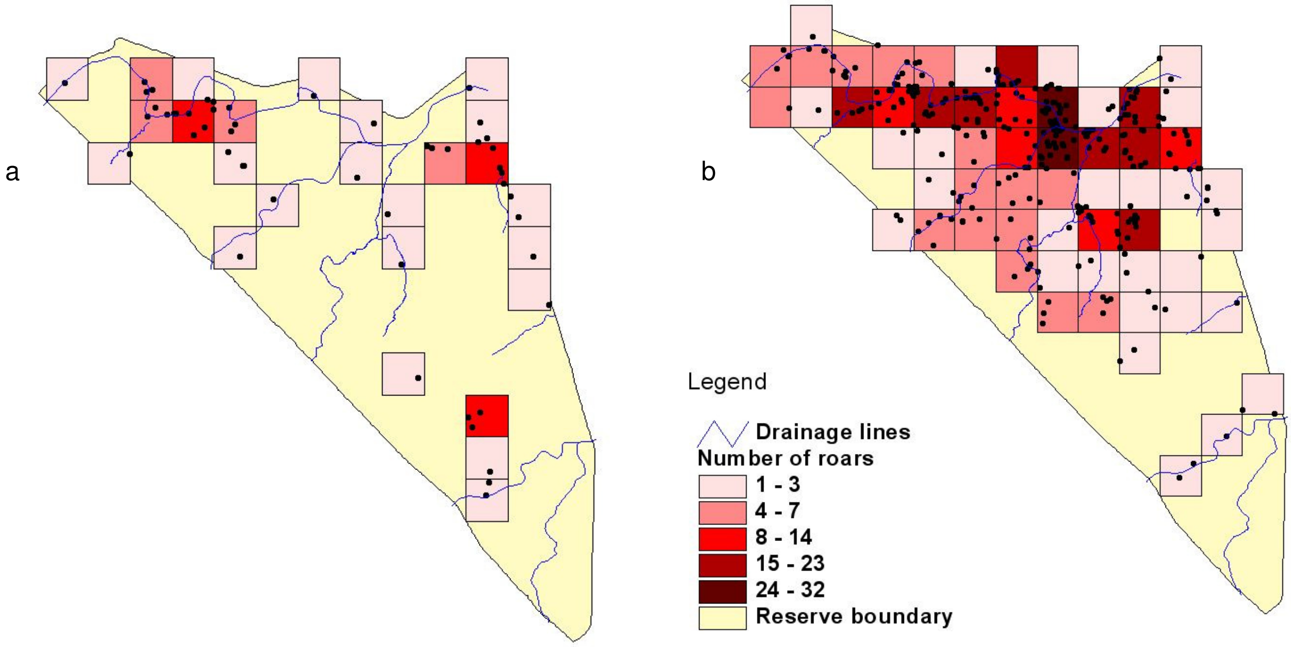


Figure 3.6. Locations of roars made (a) by the pride males from 1999 to 2002 and (b) by the single male from 2002-2005, indicating the frequency of roars across the reserve

3.4 DISCUSSION

3.4.1 Home range expansion

The home range of the lion pride on Karongwe almost doubled in size in the years subsequent to the reintroduction year, but remained constant according to Minimum Convex Polygons (MCP) illustrating the coarse nature of MCP to access home ranges. This was possibly because during the first year the lions were still exploring the reserve. Lion home range sizes vary considerably across study areas, ranging from 20-45 km^2 in places like Manyara National Park and Ngorongoro Crater (Schaller 1972; Hanby & Bygott 1987) and from 150-2075 km^2 in arid ecosystems such as Etosha National Park (Stander 1991). Even a study on the neighbouring reserve, Makalali, showed variability with home ranges varying from 24.9 km^2 to 106.8 km^2 (Druce *et al.* 2002b). The figures for Karongwe were intermediate between those of the seasonal home range changes on Makalali. On the central and southeastern basalt regions of the Kruger National Park the home ranges of lions are about 100 km^2 (Whyte 1985; Funston 1999), whereas they are about 250 km^2 on the northern basalt plains (Funston 1997). Both studies on small reserves thus indicated that lion prides in the Lowveld adjacent to the Kruger National Park do not necessarily need extensive areas for their home range, with prides in these smaller reserves having smaller home ranges on average to those recorded in the Kruger National Park. It must be noted that the range available to the lions on Karongwe was larger than the range utilised. This could be due to both resource and social limitations, which will be explored later in the discussion.

3.4.2 Home range utilisation

Rivers are important in lion home ranges as lions require access to safe denning sites and prefer access to water (Hunter 1999). Lion in the Selous Game Reserve also showed preference for riverine habitats (Spong 2002). Van Orsdol *et al.* (1985) and Spong (2002) suggested that home range size in lions is driven mostly by prey availability rather than habitat composition. Van Orsdol *et al.* (1985) noted that the summer core areas were smaller than the dry season core areas. McNab (1963) also expected home ranges to be larger during cold seasons. Unlike these studies in the Serengeti, results in this study compare with those on Makalali, where home ranges were smaller in winter than in summer, with a more concentrated core range (Druce *et al.* 2002b). The migration of prey animals in the Serengeti ecosystem is probably the reason why home ranges there are larger in winter, as the prey is more widely dispersed and lions need to venture farther to hunt. Both Karongwe and Makalali are small reserves where prey can not migrate and is always confined within the reserve. The only difference will be that prey moves closer to water in winter causing the lions' home range to contract and focus on drainage lines.

The fact that there was no significant change in home range size before and after the one male was removed was not surprising, as the same pride was still present and the male still had to defend the same territory within the reserve.

3.4.3 Response to resource and social factors

Some studies have suggested that home range size is influenced by patterns of resource distribution (Bradbury & Vehrencamp 1976; Macdonald 1983), or by social effects (Spong 2002). Considering grid preference and habitat use, it is evident that the males and subadult males were not affected by the pride to the east as they utilised the buffer area at its availability. The males therefore seemed to utilise the resources of their home range regardless of social influence. The females, however, were shown to avoid the area, therefore displaying a response to the social influence from the east. This could be due to the fact that females and their cubs are more violently affected by incoming males (Grinnell & McComb 1996) and were avoiding the area to prevent contact with potentially infanticidal males. Pusey and Packer (1987) have shown that new prides often settle adjacent to their natal range and this suggests tolerant behaviour from former pride mates. The females on Karongwe did originate from Makalali, and the neighbouring pride is therefore their natal pride. Nevertheless they did not seem to show tolerant behaviour. Lion distribution was therefore found to be affected by social limitations of neighbouring prides in females, but not so for the males. Although a random distribution was expected in the case of distribution affected by resource limitations, this was not the case due to the strong preference for drainage lines and water. These areas were found to be preferred by all groups. This could be largely due to prey availability, cover and protection for cubs, particularly as the area was most strongly preferred by the lionesses. Male ranges and to a lesser extent female ranges were therefore dictated by the resources of the area, particularly by the presence of drainage lines.

3.4.4 Movement patterns

As cloud cover and the phase of the moon did not directly affect movement it can be assumed that lions hunt and patrol their territories on both light and dark nights. However, the time of night affects how light the sky is during a particular phase of the moon and this combination seems to be important. As the male walked the furthest on a full moon between 21:00 – 04:00 when the sky is the brightest and the least during new moon in the early hours of the night when the sky is the darkest indicates that the amount of light nights seems to be important for territorial patrols.

3.4.5 Territorial behaviour

These results showed that the pride male did most territorial patrolling while alone, when he could cover more distance. In so doing he possibly prevented putting pride members at unnecessary risk in the event of an encounter. Although the study focused on the pride male, lionesses were also observed to scent mark and roar, but usually while together or in the presence of the pride male. This is because when female lions roar they increase their risk of attracting potentially infanticidal males (Grinnell & McComb 1996), and by roaring in groups they minimise such encounters. Funston (1999) also noted that a lot of territorial behaviour occurs along drainage lines. This could be because rivers are often natural borders between home ranges and water points are likely to be highly contested areas. It was found that drainage lines were preferred to the rest of the reserve by the lions on Karongwe and were therefore the most important resource in the home range. Although the males were found to utilise the buffer zone at its availability, the coalition showed preference for both scent marking and roaring in this area. This was probably due to the social influence from the east, causing males to concentrate on this area for their territorial displays. The single male showed a weak preference for scent marking in the buffer zone probably for the same reason, but used the buffer zone just below availability for roaring bouts. This slight avoidance of roaring in the buffer zone could be because as a single male he did not want to advertise the fact that he was alone, which would make it potentially easier for incoming males to contest his territory.

3.4.6 Scent marking by the pride male

The pride male scent marked less frequently than the average coalition in the Kruger National Park who was found to deposit 2.6 scent marks/km (Funston 1999). The same study in the Kruger National Park showed that a singe male deposited more scent marks per kilometre and per night to match the rate of a coalition. Funston (1999) suggested that this indicates a minimum rate at which territorial males mark to gain a pride and discourage other males. The fact that the Karongwe male marked less frequently could indicate that because he was in a small fenced reserve that he did not think his territory was under threat from other males. The rate would possibly increase if other males were present or if the fences were dropped between reserves.

3.4.7 Territorial roaring by the pride male

During all observations the single male roared slightly less than a coalition in the Kruger National Park (0.8 roars/hour) and considerably less than the single male from the Kruger National Park who made 1.4 roars/hour (Funston 1999). However, when the male was away from the pride females he roared at a rate higher than even the single male from the Kruger National Park. Males treat opponents that roar as a serious threat as only residents roar and are likely to chase and attack rivals (Grinnell, Packer & Pusey 1995). It is possible therefore that he still roared frequently to dissuade potential intruders from farther away from approaching his territory boundary.

3.5 CONCLUSION

This study has illustrated the importance of rivers and drainage lines to the establishment of a lion population. Whether there are two males or only one male does not alter the home range utilisation of the lions. Territorial behaviour seems to be reduced slightly due to the lack of conspecific competition on the reserve. Of particular importance is the finding that resources affect the distribution and home range use of male lions, and social factors affect territorial behaviour. Female lions also seem to respond to resource factors, but respond more strongly to social factors from neighbouring lions. These implications are important when reintroducing lions to new areas, and can aid in the management and planning for the conservation of these predators.

CHAPTER 4

REPRODUCTIVE BIOLOGY

4.1 INTRODUCTION

Reproduction is essential for the prevalence of a species and it is therefore important to understand a species' reproductive parameters in order to conserve it. Several studies in larger systems have found that females in a pride tend to come into oestrus simultaneously and give birth synchronously (Bertram 1975a), typically having their first litter at three to four years of age (Packer *et al.* 1988), and on average two to three cubs (Van Orsdol, Hanby & Bygott 1985). Certain parameters such as these and age of first reproduction, birth rate and inter-birth intervals are very important to consider on small reserves and may well be significantly different from those in large open systems.

Without intra-specific competition it was hypothesised that individuals might reproduce for the first time at a younger age, and have a higher birth rate, thus influencing their management. An increased birth rate can have a significant effect on a population confined in a small area, and it is therefore imperative to carefully monitor the reproductive biology and behaviour of reintroduced lions (*Panthera leo*) (Peel & Montagu 1999; Power 2002a; Druce *et al.* 2002b).

4.2 METHODS

The general methods described in Chapter 1 were used to locate the lions and record data. All behaviour that was reproductive in nature was recorded, including oestrus cycles, mating, and all behaviour related to cubs and their upbringing. An oestrus cycle was defined as days on which the female was mating (Packer & Pusey 1983b). The mating date was always known due to direct observations at the time, but the exact birth date was estimated to be around the time the female localised and spent a large portion of her time in a given area. For the purposes of this study, the two lionesses monitored were named F1 and F2.

4.3 RESULTS

4.3.1 Reproductive parameters

Table 4.1. Parentage and gender of all cubs born on Karongwe

Lioness	Birth date	Father	Sex	Age at translocation / death	Translocation date	Date of death
F1						
	Jun-00	Zero	M	17 months	Nov-01	-
	Jun-00	Zero	F	17 months	Nov-01	-
	Mar-02	Felix	M	26 months	May-04	-
	Mar-02	Felix	M	26 months	May-04	May-04 (twisted gut)
	Jan-04	Zero	M	-		-
	Jan-04	Zero	F	25 months	Feb-06	-
	Jan-04	Zero	F	25 months	Feb-06	-
	Dec-05	Zero	M	-	-	-
	Dec-05	Zero	F	-	-	-
	Dec-05	Zero	?	*1 month*	-	Jan-06
F2						
	Dec-00	Zero	M	27 months	Mar-03	-
	Dec-00	Zero	M	27 months	Mar-03	-
	Aug-02	Felix	F	19 months	Mar-04	-
	Aug-02	Felix	M	3 yrs 8 months		Apr-06 (hunted)
	Aug-02	Felix	M	3 yrs 8 months		Apr-06 (hunted)
	Aug-04	Zero	?	*1 month*	-	Sep-04

Since the introduction of four lions in 1999 sixteen cubs in seven litters were born (Table 4.1). The pride had an increase of 350% in six years. Thus the growth rate of the pride on Karongwe was 25% per year.

Their mean litter size was 2.3 (n = 7), with a birth rate of 1.3 cubs/lioness/year. The two lionesses had an average interbirth interval of 22 months (range: 19.5-24; n = 5). Although one female (F1) had longer intervals than the other, this difference in interbirth intervals was not significant (ANOVA, $F_{1,3} = 0.047$; NS, SE = 0.82). There was no significant difference in the sex ratio of cubs at birth, although it was slightly male biased with 1♀:1.8♂ (n = 14 sexed cubs) ($\chi^2_1 = 0.84$ NS).

Table 4.2. Comparison of reproductive parameters on Karongwe and other studies. Adapted from Rudnai (1973)

	Karongwe	**Makalali**	**Welgevonden**	**Kruger**	**Serengeti**
Source		**(Druce *et al.* 2002)**	**(Killian & Bothma 2003)**	**(Smuts *et al.* 1978; Funston *et al.* 2003)**	**(Schaller 1972)**
Age at first conception (months)	38	43	41	43-56	42-54
Age of males' first successful mate (months)	34		38	78	
Mating success (%) *	8				20
Inter-birth intervals (months)	22	22	17	40	22-26
Mean litter size	2.3	2.9	2.8	3.0	2.3
Reproductive potential realized (% reached 2 years)	88	100	85	80	13

* Mating success refers to the percentage of observed matings that resulted in conception

Cubs were not seen at the time of birth but only when they were a few weeks old. Only two known cubs died during the study, and therefore 88% of cubs seen after birth (n = 16) reached the age of two years. Males and females bred at a younger age but mating success was lower than in other studies (Table 4.2).

4.3.2 Oestrus cycles and mating success

Oestrus duration and intervals were highly variable. F2 had 64 oestrus cycles while F1 only had 23 cycles over the same time period. F2 had longer and more frequent oestrus cycles but was also less successful at conceiving (Table 4.3). These differences in oestrus duration between the two females was significant (ANOVA, $F_{1,85} = 4.747$; p = 0.03, SE = 0.19) (F1 range 1-4 days; F2 range 1-7 days). The difference in oestrus intervals was highly significant (ANOVA, $F_{1,83} = 9.725$; p = 0.002, SE = 9.59). The average oestrus interval for both females was 42.9 ± 10.46 days (range 2-514, n = 74). (F2: 28.0 ± 6.99 days (range 2-367, n = 58) and F1: 97.1 ± 39.24 days (range: 2-514, n = 16).)

Table 4.3. Oestrus cycles and mating success of the lionesses on Karongwe

	Lioness 1	**Lioness 2**	**Sum**
Number of cycles	23	64	87
Average duration of oestrus (days)	1.4	2.3	1.9
Average inter-oestrus interval (days)	97.8	32.8	65.3
Successful cycles (%)	4 (17.4)	3 (4.7)	7 (8.0)
Cycles while pregnant (%)	3 (13.0)	3 (4.7)	6 (7.0)
Cycles while lactating (%)	4 (17.4)	8 (12.5)	12 (13.8)
Short 1 or 2 day cycles (%)	20 (86.9)	45 (70.3)	65 (74.7)
Successful short cycles (%)	2 (10.0)	1 (2.2)	3 (4.5)
Successful long cycles (%)	2 (66.7)	2 (10.5)	4 (18.0)

Of the total 87 oestrus cycles of the two lionesses, only eleven cycles overlapped. Only one female fell pregnant in one of those cycles and therefore very little oestrus synchrony and no birth synchrony occurred on Karongwe.

The fact that a lioness was pregnant, or had young cubs, did not prevent her from coming into oestrus and mating (Table 4.3). F2 mated on average 53 ± 29.7 days after conception (range 32-74, n = 2), and F1 mated 108 ± 96.2 days after conception (range 5-215, n = 4). The lionesses also continued to mate while they were lactating. The first successful mating occurred when the previous cubs were 18.2 ± 1.8 months old (range 15.8-20.23, n = 5). When the whole litter was lost, as was the case on one occasion, the female mated 15 days after the cub was born but waited four months after it died until she mated again. Mating success was generally low with only 8% (n = 87) of all mating periods resulting in conception (Table 4.3). Of the unsuccessful matings 6.9% occurred while the female was pregnant, and 13.8% while lactating. A total of 87 mating cycles were recorded, of which most (74.7%) were short 1 or 2 day cycles, with only 4.5% of these being successful. Longer cycles (3-7 days) comprised only 25% of cycles, but were significantly ($\chi^2_1 = 4.09$, $p < 0.05$) more successful, with 18% of these resulting in conception.

Following the removal of one of the adult males in 2002, F2 only conceived once by the end of 2005 and did not successfully raise the single cub that was born. Subsequently she came into oestrus regularly. During the same two-year period F1 raised two litters successfully.

4.3.3 Male mating behaviour and male scenarios

The males were introduced into a male free environment at 18 months of age. One male was removed after 32 months, and by the end of 2005 the single male had been in the reserve for 72 months. The average age of the males at their first successful mate was 2.8 years (n = 2).

Both males were observed to father litters and alternated between mating opportunities. Despite the fact that the pride had no interspecific competition, mate guarding did occur both when two males and the single male were present. There was no significant difference in the amount of observed mate guarding that took place before (100%) and after (94%) the coalition was split (ANOVA, $F_{1,53} = 2.34$, NS, SE = 0.074). The presence of subadult males could also have prompted mate-guarding.

4.3.4 Lioness behaviour and dependence of cubs

Cubs were first seen at 36 days of age (range 16–60 days, n = 14), and were first introduced to the pride when they were 53 days old (range 43–74 days, n = 14). Except for the first litter, there were always older cubs present when these young cubs were introduced.

Cubs became gradually less dependent on their mothers and were first observed to be alone at 10 months of age (range 6–12 months, n = 11), although at this age they still spent the majority (96.8% ± 2.62 observations) of their time with the pride. Between 10 and 18 months of age they spent an increasing amount of time alone (5.9% ± 3.91), and started hunting. Typically subadults were removed from the reserve at 26 months of age (range 17-44, n = 11).

4.4 DISCUSSION

4.4.1 Population demography and reproductive parameters

The average age of the first successful conception was 38 months, which was slightly lower than figures cited for large reserves such as the Kruger National Park (Smuts, Hanks & Whyte 1978), or the Serengeti (Schaller 1972; Packer *et al.* 1988). The lack of competition on Karongwe could be the reason that sexual maturity and age of first reproduction was reached at a younger age when compared with reserves such as the Kruger National Park. The younger age of first reproduction is directly comparable with that of other reintroduced lion populations in small reserves in South Africa (Killian & Bothma 2003, Druce *et al.* 2002b) where competition was also low.

The mean litter size was similar to that recorded by Schaller (1972), Bertram (1975a) and Van Orsdol et al. (1985) in east Africa, but was lower than the median litter size of three in the more comparable Kruger National Park (Smuts et al. 1978; Funston et al. 2003). Litter sizes in other small reintroduced lion populations in South Africa are also around three (Killian & Bothma 2003, Druce et al. 2002b). Litter sizes could be smaller on Karongwe due to the small size of the reserve and subsequent predator pressure due to the high number of other predators, causing females to produce less offspring than in the large open system found in the Kruger National Park. It is also possible that more cubs were killed before they were seen by researchers. The low litter sizes on Karongwe might, therefore, be an anomaly because only two lionesses were involved, one of which showed atypical interbirth intervals, or that the extremely small size of Karongwe prompted smaller litters.

The birth rate recorded here (1.3 cubs/lioness/year) was higher than the rate of 0.77 cubs/lioness/year in Etosha (Orford *et al.* 1988) and 1 cub/lioness/year in the Kruger National Park (Funston *et al.* 2003), but was lower than the rate of 1.9 in Welgevonden Private Game Reserve (Killian & Bothma 2003) and 2.3 cubs/lioness/year in Makalali (Druce *et al.* 2002b). Here again Karongwe was slightly dissimilar to other small reserves in South Africa. Nevertheless the growth rate was higher than that in large reserves and thus conforms to the pattern found in other small reserves (Vartan 2001; Killian & Bothma 2003; Funston & Jolley in prep.). However, the increased birth rate on Karongwe is countered to some extent by the smaller litter sizes.

The average interbirth interval of 22 months was considerably shorter than the 40 months calculated by Funston *et al.* (2003) for the Kruger National Park, and was two months shorter than the 24 months calculated in east Africa (Rudnai 1973, Bertram 1975a, Packer & Pusey 1987). However, it falls within the range of those calculated on other small reserves with reintroduced prides (Killian & Bothma 2003; Druce *et al.* 2002b).

Cub mortality at Karongwe was a lot lower than the Serengeti Plains, where the lack of prey when the migratory herds are absent causes high rates of cub starvation, with more than half of the cubs born dying before they reach one year of age (Schaller 1972; Rudnai 1973; Packer & Pusey 1983a). A similarly high rate of cub survival, however, has been recorded in other small reserves (Druce *et al.* 2002b; Killian & Bothma 2003), as well as in the Kruger National Park (Funston *et al.* 2003). The migratory nature of the prey and the low survival rate of cubs could be the reason why lions in east Africa have shorter inter-birth intervals when compared with the stable conditions and high survival rate in the Kruger National Park. The stable conditions and reduced competition on small reserves seems therefore to shorten inter-birth intervals, at least when compared with the Kruger National Park.

The sex ratio at first visual after birth was different to many other studies that have observed an equal sex ratio in both captive and wild populations (Rudnai 1973; Smuts *et al.* 1978; Druce *et al.* 2002b). The sex ratio on Karongwe favoured almost twice as many males as females at birth. Bonato (2001) proposed that lionesses give birth to more male cubs when in good condition, and that females should reduce competition among their cubs by having more male offspring as these will disperse from the natal site. More male cubs are born just after a takeover by new males and in areas where males are hunted or otherwise removed from an area (Packer & Pusey 1987). The removal of one adult male, small size of the reserve, and continued removal of subadults, probably contributed to the bias towards male cubs.

4.4.2 Oestrus cycles and mating success

The variation and irregularity in oestrus cycle duration and intervals that we observed has also been observed in other studies (Schaller 1972; Rudnai 1973; Bertram 1975a; Packer & Pusey 1983b), but generally lions display oestrus cycle and birth synchrony (Schaller 1972; Bertram 1975a; Packer & Pusey 1983b; Funston *et al.* 2003). This tends to result in cubs being born in the same or adjacent months (Bertram 1975a). This was not the case on Karongwe. It was suggested by Packer and Pusey (1987) that cohorts of synchronously born cubs may only be important when competition is present, and that cubs born later in the tenure of a new male are less likely to be born synchronously with cubs of other females (Packer & Pusey 1983a). This explanation seems to fit the patterns observed at

Karongwe, but it could also be that small sample sizes and apparent aberrant behaviour by one of the lionesses may confound the explanation.

The low mating success was consistent with other studies (Schaller 1972; Rudnai 1973; Bertram 1975a), although the figure on Karongwe was considerably lower than the 20% in the Serengeti and 50% in Nairobi (Schaller 1972; Rudnai 1973). The reason for this could be F2's inability to conceive or raise a litter after the second adult male was removed. Several explanations could be given for the lack of reproductive success of F2, including higher cub mortality due to increased predator numbers since 2002, or that she was less proficient at hiding her cubs. The high incidence of reproductive failure may be due to anovulatory cycles (Smuts *et al.* 1978). Abortion or psuedopregnancy could also be a possibility. No definite pseudopregnancy or false pregnancy had been previously recorded although a study in the Kruger National Park showed two sterile ovulations seemed to be followed by pseudopregnancies (Smuts *et al.* 1978), and also showed that lionesses can resorb foetuses. Without more data it is difficult to be conclusive about this.

4.4.3 Male mating behaviour and male scenarios

Due to the fact that the males were introduced into an area with no competition they began their tenure at a much younger age than the usual five or six years of age (Rudnai 1973; Smuts *et al.* 1978; Funston *et al.* 2003). This is not atypical for lions in reintroduced populations without older males present (Killian & Bothma 2003; Hunter 1998). Males are sexually immature until they reach about 26-30 months of age, but generally do not mate before the age of five years (Smuts *et al.* 1978). Early mating is thus possible in the absence of older male lions.

There is generally no detectable hierarchy within coalitions of male lion groups (Bygott, Bertram & Hanby 1979), as was observed on Karongwe where both males fathered litters and alternated between mating opportunities. As the males guarded their mates it would seem that this is an instinctual behaviour, although within coalition competition and the presence of the subadult males (although sexually immature), might be more important during mating than the perceived threat from nearby, but fenced-off, lions on an adjoining property.

4.4.4 Lioness behaviour and dependence of cubs

The subadults became independent earlier (10-18 months) than expected from other studies, where subadult males generally emigrated from 27-42 months, and females from 21-31 months (Schaller 1972; Bertram 1975a; Smuts *et al.* 1978; Hanby & Bygott 1987). Dispersal was even more protracted in the nearby Kruger National Park, where subadult males finally dispersed at 48 months of age (Funston *et al.* 2003). When the Karongwe subadults were only half this age they already spent substantial amounts of time away from the pride, and most had been translocated before the age that subadults in other areas only begin leaving the pride. Resources were more constant on Karongwe and therefore food was easier to find throughout the year than in the Serengeti, allowing subadults to hunt for themselves successfully at a younger age. Although the resources in the Kruger National Park are much the same as on Karongwe, subadults on Karongwe are able to leave the pride at a younger age due to the lack of competition particularly from other males.

4.5 CONCLUSION

Although much work has been undertaken on the reproductive behaviour of lions, this study illustrates the implications of having a reintroduced pride of lions on a very small reserve. In reserves where there can only be one small pride, and thus little or no conspecific competition, lions may breed at a faster rate than in wild populations and subadults move away from the pride at an earlier age. Age at first breeding is lower when there are no dominant lions to suppress others, increasing the effective reproductive potential of female and particularly male lions.

CHAPTER 5

FEEDING BEHAVIOUR

5.1 INTRODUCTION

All animals require food in order to sustain them and to reproduce, allowing the species to remain in that area. Carnivores need their prey requirements to be met on small reserves, as there is no chance of migrating in search for better or more food. Reserve managers therefore need to ensure that the reserve is stocked with not only the correct prey species, but also the correct number of each species. Understanding what lions on small reserves feed on will enable managers to make more informed decisions, not only regarding prey species, but also how many lions to reintroduce and what their population structure could be.

This study focuses on a single pride of lions in order to determine the prey requirements of one pride and its related males in an enclosed reserve that was effectively their home range. As the population experienced no intraspecific competition it was an ideal scenario in which to study the food requirements of a small population, and as many such reserves exist in which lion reintroductions have, or will, occur these results should be applicable to those populations.

5.2 METHODS

The general methods described in Chapter 1 were used to locate the lions and record general data. All information pertaining to kills and feeding behaviour was recorded. The species, age class, and gender of any kill found were noted using ageing and sexing criteria set by McBride (1984). If a kill was present, but not visible, the site was revisited once the lions had vacated the area, and the carcass located and identified. The individuals present at each kill were noted, and where possible the lion that made the kill was identified and recorded.

The prey base was enumerated using aerial counts. A Bell Jet helicopter was flown in a grid pattern over the whole reserve using the same crew at the same time of year, every year. Annual aerial census figures from 1999 to 2005 were obtained to show the fluctuations in ungulate numbers on Karongwe. These figures showed a sharp decline in impala and waterbuck numbers towards the end of the study period, while giraffe and kudu remained relatively stable (Figure 5.1).

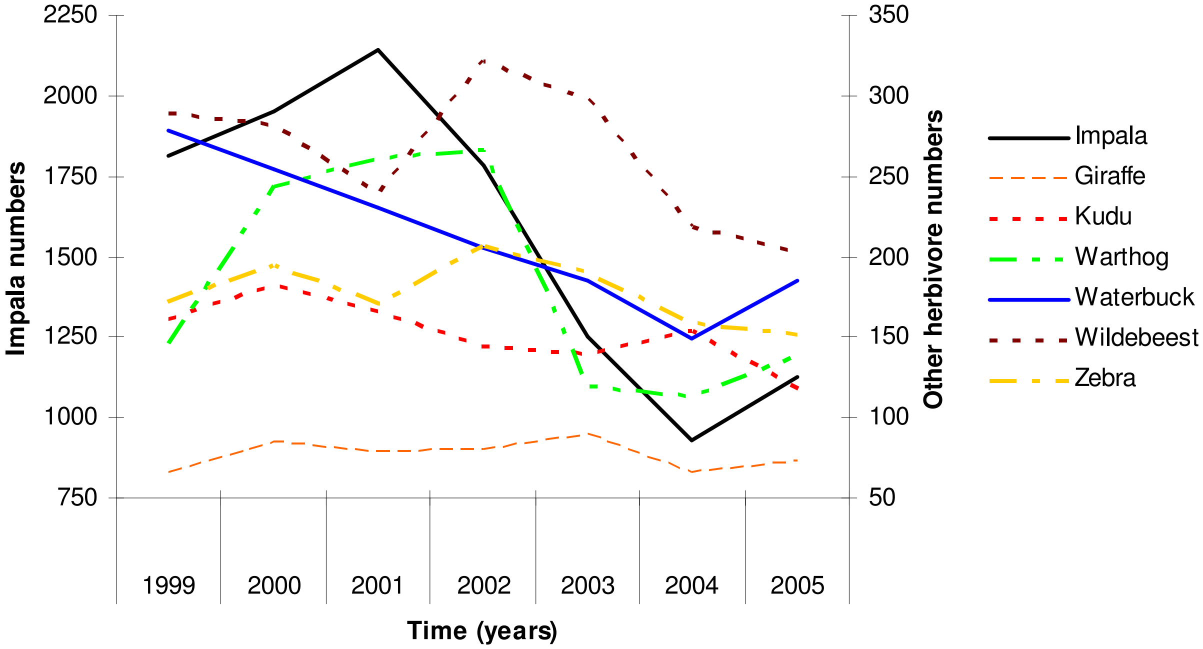


Figure 5.1. Fluctuations in prey numbers on Karongwe Game Reserve, obtained from annual aerial game censuses between 1999 and 2005. (Small amounts of giraffe, kudu, warthog, waterbuck and zebra were removed over the years, particularly in 2004. Wildebeest were supplemented in 2002 by adding 75 individuals)

5.2.1 Data analysis

All data were entered into a spreadsheet and a condensed table indicating group composition and daily belly scores (Bertram 1975b) was compiled. This enabled the allocation of missed kills using substantial increases in belly score as an indicator of a kill having taken place. This is probably thus a conservative estimation as small kills would not necessarily have been accounted for. The total number of kills made, including those inferred by belly size change, was used to determine the kill rate. For all other analyses only the observed kills were used.

Individual lions were only regarded as being part of a group if they could be seen or if there was a strong radio-signal from a collared individual (i.e. nearby, but not seen. Researchers waited for an average of 30 minutes to ensure visual could not be obtained). Lion Feeding Units (LFUs) (Van Orsdol 1981) were assigned in order to take the age and size of the lions into account when determining the proportion of food each lion eats. This classification assumes that adult males eat 1.5 times as much as females, and large cubs (2-3 years) eat 0.75 times that of adult lionesses, medium cubs (1-2 years) eat 0.5 times the amount, and small cubs eat 0.25 as much as an adult lioness.

5.3 RESULTS

5.3.1 Group composition and estimated number of kills made

The pride was located with all current members and males together relatively seldom (18.8%, n = 381), with the two pride males being away from the pride at many of the locations (44.9% of total male locations, n = 389). However, when the one male was removed the remaining male was found away from the pride significantly less frequently (12.7%, n = 265, $\chi^2_1 = 194$, $p < 0.01$).

It was estimated that 1539 kills were made over the six year period, but only 43% (n = 662) of these were located, of which 591 could be identified to species. See Table 5.1 for a breakdown of kills found and thought to have occurred. During the tenure of the male coalition (988 days) these males made 33.2% (n = 96) of all the kills found while the females killed 44.3% (n = 128) while alone and 22.5% (n = 65) were made with males and females together. In the latter period (1130 days) when one male was removed the single male killed 4.9% (n = 17), the females 20.5% (n = 71) and together they killed 60.9% (n = 211) of all kills. Significantly less kills were made by the single male than expected when compared with the kills made by the coalition and by the females (χ^2_1 = 180.77, $p < 0.01$). The females made an estimated 381 kills while the coalition was present and 676 estimated kills after one male was removed. Of those 312 kills actually found to be made by the females during the later period, 33 (10.6%) were fed on only by the adult females; cubs and subadults with adult females fed on 57 kills (18.3%); and adult females, cubs and the single male were present at the majority of kills (222 kills; 71%). In the latter period dispersing subadult males made 17.6% (n = 159) of all the kills estimated to have occurred. The dispersing subadult males were significantly more likely to make kills on their own (n = 159) than the single territorial male (n = 69, χ^2_1 = 35.52, $p < 0.01$), but made significantly less kills than the paired coalition (n = 254) (χ^2_1 = 21.86, $p < 0.01$). The presence of the second pride male had a significant effect on the total number of kills (ANOVA, $F_{1,67}$ = 13.676, $p < 0.001$, SE = 0.64), and the number of kills made by males (ANOVA, $F_{1,67}$ = 33.901, $p < 0.001$, SE = 0.23).

Table 5.1. Summary of kills found and estimated, and an average of kills made per lion or pride

Year	Average number of lions	Average number of LFUs*	Estimated kills per annum	Kills located (%)	Estimated number kills/month	Number kills/adult lion/ month	Number kills/ adult lion/ year	Number of kills/ LFU
2000	4.5	5	214	98 (46)	17.8	4.5	54	43
2001	7.5	5.7	226	100 (44)	18.8	4.7	57	40
2002	7.3	6.1	289	138 (48)	24.1	6.4	77	47
2003	8.8	6.0	268	124 (46)	22.3	7.4	89	45
2004	8.8	6.6	299	101 (34)	24.9	8.3	99	45
2005	8	7.5	243	101 (42)	20.3	6.7	81	33

* Lion Feeding Unit as taken from Power (2002a). See text for a full explanation

Collectively the lions made an average of 42 kills per LFU per year (Table 5.1), with an average of 21 kills per month. The number of kills made in the first period equated to a combined kill rate of one kill every 1.6 days, with the pride males making a kill every 3.9 days, and the pride females killing once every 2.6 days. However in the latter period pride females were estimated to make a kill every 1.7 days, with the single pride male only killing once every 16.4 days. Although the pride females did not make significantly more kills per day in the latter as compared with the earlier time period ($\chi^2_1 = 0.188$, NS), the male's estimated kill rate was significantly more when the paired coalition was present ($\chi^2_1 = 7.67$, $p < 0.01$).

There was a significant modest positive correlation ($r_s = 0.40$, $n = 69$, $p > 0.01$) between the number of kills made and population size (expressed as LFUs). The number of LFUs varied greatly with each lion social group. The single male and subadult coalitions had the lowest LFU per group and the largest group was the mixed group after 2002. When comparing kill rate and LFU there is little increase in kills as LFU's increase (Table 5.2).

At 5 LFU the kill rate was 1.55 and at 8.25 LFU the kill rate was 1.57 (range: 5 - 8.25 LFU and 1.17 – 1.75 kill rate). A weak positive correlation (Spearman Rank Correlation Coefficient: $r_s = 0.20$, $n = 105$, $p < 0.01$) existed between the number of kills and the age of cubs. The correlation between LFUs and biomass killed was not statistically significant, although this may have been a consequence of low statistical power, and there may be a weak biological positive correlation (Spearman Rank Correlation Coefficient: $r_s = 0.27$, $n = 9$, NS).

Table 5.2. Number of kills found per Lion Feeding Unit (LFU) for each social group

Lion group	Number of kills	LFUs	kill / LFU
With coalition present			
Coalition	96	3	32
Females alone	128	2	64
Mixed group (adult males with females)	65	5.5	12
With single male present			
Single male	17	1.5	11
Sub-adults	47	1.5	31
Females alone	71	2	36
Mixed group	211	7.5	28

* Lion Feeding Unit as taken from Power (2002a). See text for a full explanation

The lions killed between 3.3 - 7.1% of available biomass (Table 5.3). The range of biomass killed per LFU per year was 2530.9 kg – 4419.5 kg, which translated to 6.9 – 12.1 kg / LFU / day.

Table 5.3. Biomass available on the reserve and amount of biomass killed per LFU

Year	Available biomass (kg)	Biomass killed (kg)	% biomass killed	LFUs	Biomass (kg) killed / LFU / year	Biomass (kg) killed / LFU / day
2000	444 136	14 712	3.3	5	2 942	8.0
2001	420 523	15 252	3.6	5.75	2 652	7.3
2002	420 513	23 893	5.7	6.13	3 897	10.7
2003	374 678	26 517	7.1	6.0	4 419	12.1
2004	297 257	19 965	6.7	6.63	3 011	8.2
2005	310 650	19 083	6.1	7.54	2 530	6.9

* Lion Feeding Unit as taken from Power (2002a). See text for a full explanation

5.3.2 Effect of season

Most kills were found in October (n = 75), and the least in April (n = 41). There was a significant difference in the number of kills made in the different seasons (ANOVA, $F_{2,9} = 6,140$) with most kills made in the hot dry season from September to November.

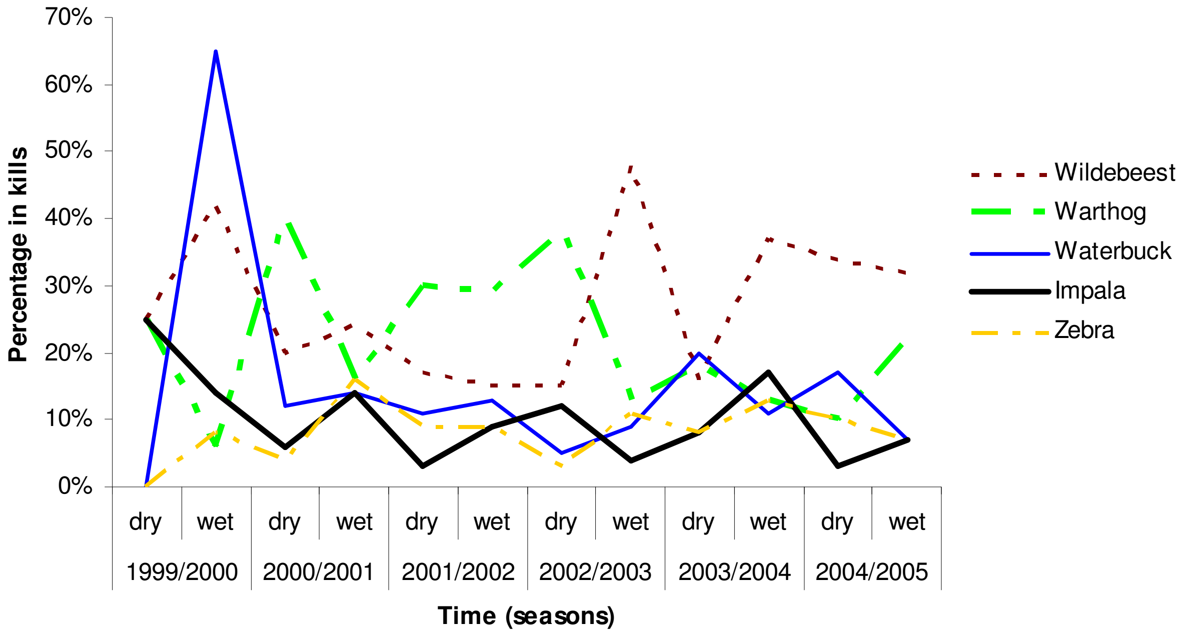
5.3.3 Prey selection

The lions preyed on 21 species (Table 5.4), five of those comprised 72.1% (n = 591) of all kills found, with wildebeest (24.2%, n = 143), warthog (20.1%, n = 119), waterbuck (11.3%, n = 67), impala (8.5%, n = 50) and zebra (8.0%, n = 47) being the most important species. Figure 5.2 shows the fluctuations of these five species as a percentage in kills compared with the actual number of kills per species. The difference between observed and expected species killed per season was significant ($\chi^2_1 = 20.62$, $p < 0.01$).

Table 5.4. All species killed by the lions during the study period (n = 591)

Species	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**Total (%)***
Small prey/other							
Aardvark			1		2		3 (0.5)
Bushpig	2	1	3	1	2	1	10 (1.7)
Civet		1					1 (0.2)
Duiker		1	1				2 (0.3)
Ostrich	7						7 (1.2)
Porcupine	2	1	1			1	5 (0.8)
Tortoise		2	1		1	2	6 (1.0)
						Total	**34 (6)**
Small (40-100 kg) ungulate prey							
Bushbuck	5	6	12	5	1	3	32 (5.4)
Impala	8	7	7	9	11	8	50 (8.5)
Nyala	2			1	2	1	6 (1.0)
Warthog	17	18	34	23	14	13	119 (20.0)
						Total	**207 (35)**
Medium-large (> 100 kg) ungulate prey							
Cow			2			1	3 (0.5)
Eland	1						1 (0.2)
Gemsbok	1	1	1				3 (0.5)
Giraffe	2	1	9	10	6	5	33 (5.6)
Horse			1	1		2	4 (0.7)
Kudu	3	5	8	9	5	10	40 (6.8)
Red hartebeest	4	3	2				9 (1.5)
Waterbuck	8	17	10	14	10	8	67 (11.3)
Wildebeest	22	15	20	32	24	30	143 (24.2)
Zebra	4	11	8	8	11	5	47 (7.9)
						Total	**350 (59)**

* Figures in brackets are percentages



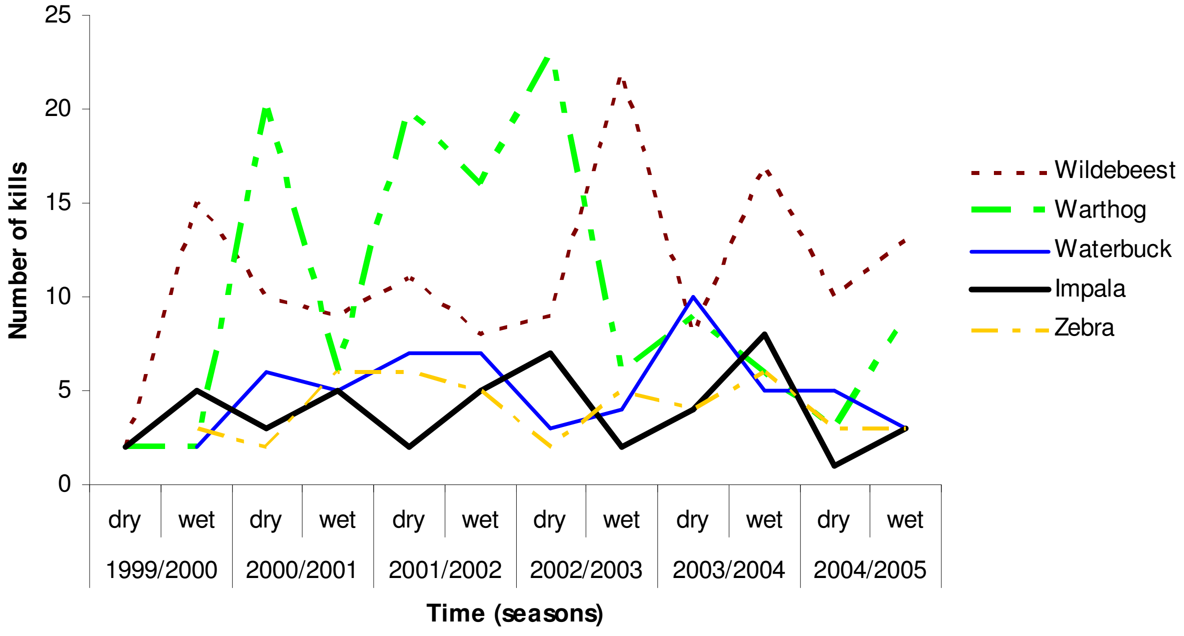


Figure 5.2. Seasonal fluctuations in the five species favoured by the lions as a percentage of lion kills recorded and as absolute numbers

No significant selection for gender was found ($\chi^2_1 = 0.47$, NS), with almost as many males (48%, n = 148) as females (52%, n = 160) being preyed upon. There was a significant selection for adult prey ($\chi^2_1 = 25.95$, $p < 0.01$) with adults making up 61% (n = 353) of all kills.

Table 5.5. Summary of all known lion kills sorted into gender and age classes and frequency each lion group fed on

	Gender						
Prey species	**Male**		**Female**		**Unknown**		
	Adult (%)	**Juvenile (%)**	**Adult (%)**	**Juvenile (%)**	**Adult (%)**	**Juvenile (%)**	**Total**
Giraffe	0 (0)	2 (7)	2 (7)	2 (7)	2 (7)	21 (72)	29
Females alone	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)	2
Females with coalition	0 (0)	0 (0)	1 (50)	0 (0)	1 (50)	0 (0)	2
Females with single male	0 (0)	2 (13)	0 (0)	1 (7)	0 (0)	12 (80)	15
Coalition alone	0 (0)	0 (0)	1 (11)	1 (11)	1 (11)	6 (67)	9
Single male alone	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	1
Impala	9 (20)	6 (13)	8 (18)	1 (2)	10 (22)	11 (25)	45
Females alone	5 (25)	3 (15)	3 (15)	0 (0)	5 (25)	4 (20)	20
Females with coalition	1 (25)	0 (0)	0 (0)	1 (25)	0 (0)	2 (50)	4
Females with single male	2 (22)	1 (12)	2 (22)	0 (0)	2 (22)	2 (22)	9
Coalition alone	0 (0)	2 (25)	3 (38)	0 (0)	2 (25)	1 (12)	8
Single male alone	1 (25)	0 (0)	0 (0)	0 (0)	1 (25)	2 (50)	4
Kudu	12 (31)	4 (10)	9 (24)	3 (8)	4 (11)	6 (16)	38
Females alone	5 (29)	1 (6)	3 (18)	1 (6)	3 (18)	4 (23)	17
Females with coalition	2 (33)	0 (0)	2 (33)	1 (17)	0 (0)	1 (17)	6
Females with single male	5 (46)	2 (18)	3 (27)	0 (0)	0 (0)	1 (9)	11
Coalition alone	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	2
Single male alone	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	2
Warthog	25 (18)	4 (3)	22 (16)	7 (5)	34 (25)	44 (33)	136
Females alone	7 (11)	1 (2)	16 (26)	1 (2)	15 (25)	21 (34)	61
Females with coalition	3 (21)	1 (7)	1 (7)	1 (7)	2 (15)	6 (43)	14
Females with single male	10 (26)	0 (0)	4 (10)	3 (8)	9 (23)	13 (33)	39
Coalition alone	4 (21)	1 (5)	1 (5)	2 (11)	7 (37)	4 (21)	19
Single male alone	1 (33)	1 (33)	0 (0)	0 (0)	1 (33)	0 (0)	3

	Gender						
Prey species	Male		Female		Unknown		
	Adult (%)	Juvenile (%)	Adult (%)	Juvenile (%)	Adult (%)	Juvenile (%)	Total
Waterbuck	22 (38)	8 (14)	10 (17)	8 (14)	6 (10)	4 (7)	58
Females alone	9 (45)	1 (5)	2 (10)	4 (20)	3 (15)	1 (5)	20
Females with coalition	2 (29)	2 (29)	2 (29)	1 (13)	0 (0)	0 (0)	7
Females with single male	8 (35)	2 (9)	6 (26)	3 (13)	1 (4)	3 (13)	23
Coalition alone	3 (38)	3 (38)	0 (0)	0 (0)	2 (24)	0 (0)	8
Single male alone	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
Wildebeest	17 (12)	7 (5)	47 (34)	10 (7)	27 (19)	32 (23)	140
Females alone	2 (5)	2 (5)	14 (35)	5 (13)	4 (10)	13 (32)	40
Females with coalition	1 (8)	0 (0)	5 (33)	2 (13)	2 (13)	5 (33)	15
Females with single male	8 (13)	4 (6)	20 (32)	3 (5)	16 (26)	11 (18)	62
Coalition alone	5 (28)	1 (6)	6 (33)	0 (0)	4 (22)	2 (11)	18
Single male alone	1 (20)	0 (0)	2 (40)	0 (0)	1 (20)	1 (20)	5
Zebra	1 (2)	0 (0)	4 (9)	2 (5)	15 (34)	22 (50)	44
Females alone	1 (8)	0 (0)	1 (8)	1 (8)	3 (25)	6 (50)	12
Females with coalition	0 (0)	0 (0)	0 (0)	1 (25)	2 (50)	1 (25)	4
Females with single male	0 (0)	0 (0)	1 (6)	0 (0)	5 (31)	10 (63)	16
Coalition alone	0 (0)	0 (0)	2 (18)	0 (0)	5 (45)	4 (37)	11
Single male alone	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	1

* Figures in brackets are percentages

Table 5.5 shows all known kills sorted into gender and age classes. The different lion subgroups (males, females, subadults, solitary individuals or mixed groups) showed no significant selection for age or gender ($\chi^2_1 = 6.53$, NS) although all were found to prefer adults or larger species. These groups did, however, select for slightly different compositions of prey in their diet (Table 5.6). Females had a slightly larger percentage of warthogs in their diet, and males and mixed groups had a larger proportion of medium- to large-sized ungulates. Both the adult male and the subadult male coalitions killed more giraffes than the other groups, while the mixed group killed fewer impalas.

Table 5.6. Percentage of the prey species found in the kills of four lion subgroups

Species	Female kills	Coalition kills	Single male kills	Subadult kills	Mixed group kills
Small prey/other					
Other	18%	13%	45%	9%	16%
Total	**18%**	**13%**	**45%**	**9%**	**16%**
Small (40-100 kg) ungulate prey					
Impala	10%	9%%	15%	15%	4%
Warthog	24%	22%	10%	12%	21%
Total	**34%**	**31%**	**25%**	**27%**	**25%**
Medium-large (> 100 kg) ungulate prey					
Giraffe	2%	10%	3%	12%	6%
Kudu	8%	2%	7%	6%	6%
Waterbuck	10%	9%	0%	9%	11%
Wildebeest	22%	22%	17%	28%	28%
Zebra	6%	13%	3%	9%	8%
Total	**48%**	**56%**	**30%**	**64%**	**59%**

Females (alone or in a pair with or without cubs); males (alone or as a coalition (in the first 3 years)); subadult males (kills made when the subadults are separated from the others); mixed groups (all kills made either as a pride or a combination of male and female individuals)

All medium- and larger-sized ungulate species were preferred relative to their abundance by the lions, (Table 5.7), especially gemsbok, warthog, red hartebeest, wildebeest, eland and giraffe. There is a statistically highly significant departure from homogeneity and therefore definite selection for certain species ($G = 476.86$, $df = 11$, $p < 0.001$). Importantly, relative to their abundance impala were not positively selected for. There was a significant difference between prey preferences when the second pride male was present and after he was removed ($\chi^2_4 = 11.66$, $p < 0.05$) where the coalition favoured more warthog and the pride killed more wildebeest after the male was removed. The lionesses and the single male favoured warthog, wildebeest then kudu, both the coalition and sub-adult groups selected for giraffe, wildebeest then warthog, and as a mixed group the lions favoured warthog, wildebeest and giraffe (Table 5.8).

Table 5.7. The lion's prey preference according to the abundance of each species

Species	Average prey preference over 6 years	2000	2001	2002	2003	2004	2005
Warthog	3.24	4.87	3.70	4.33	2.53	3.31	2.77
Wildebeest	2.72	3.28	2.22	2.49	2.79	2.03	3.00
Giraffe	2.21	1.46	0.46	3.39	2.45	2.63	1.42
Waterbuck	1.61	0.85	2.32	1.42	1.78	1.85	1.47
Zebra	1.35	1.10	1.61	1.74	1.22	1.66	0.59
Kudu	1.32	0.88	1.07	1.61	1.75	0.94	1.22
Impala	0.16	0.21	0.14	0.08	0.16	0.23	0.17

Table 5.8. The prey preference of each lion group

Species	Lionesses	Coalition	Single male	Subadults	Mixed group
Warthog	3.59	3.29	1.50	1.80	3.14
Wildebeest	2.30	2.30	1.78	2.93	2.93
Giraffe	0.74	3.68	1.11	4.42	2.21
Waterbuck	1.32	1.19	0	1.19	1.46
Zebra	0.95	2.05	0.47	1.42	1.26
Kudu	1.46	0.36	1.27	1.09	1.09
Impala	0.17	0.16	0.26	0.26	0.07

5.4 DISCUSSION

5.4.1 Group composition and estimated number of kills made

Although some studies suggest that lionesses do most of the hunting (Schaller 1972; Bertram 1978; Scheel & Packer 1991) recent studies have shown that under certain ecological circumstances males are in fact efficient hunters as well, obtaining at least half of their food from their own kills (Funston *et al.* 1998). As the coalition on Karongwe spent almost half their time alone they also made many of their own kills. However, the single male spent very little time alone indicating his reliance on females for food, as was shown in the aforementioned studies.

The amount of food consumed per LFU / day was a lot higher than the 4.6 kg / day found by Power (2002b) and similar low figures found by Schaller (1972), Viljoen (1993) and Druce *et al.* (2002a). It is also higher than the 5.3 kg / day required by an adult female (Funston *et al.* 1998), indicating that the Karongwe lions may be killing and eating more than necessary. The figures calculated by Stander (1992) in Etosha National Park and the average figure of 6.4 ± 2.2 kg / day found by Van Schalkwyk (1994) for six reserves are more comparable with the figure found in this study.

The estimated average kill rate of one kill every 2 days for lionesses compares almost precisely with that of Funston *et al.* (1998) of one every 1.8 nights for pride females in Kruger National Park. Funston *et al.* (1998) also found males to kill significantly less frequently than females. However the kill rate calculated for the single male is a lot less frequent than 1 kill / 3.2 days found in males in the Kruger National Park. This figure is however comparable with the kill rate of the Karongwe coalition.

As predicted there was a correlation between the number of kills made and the number of feeding lions (LFUs) present. This is an important finding in terms of predicting prey killing rates in determining the impact of lions on prey populations both in small and larger reserves.

The study showed a weak positive correlation between the number of kills and cub age. Although less significant than expected, it does indicate that as the cubs grow older they require more food resulting in more kills.

The lions on the neighbouring reserve, Makalali, killed between 0.9 – 3.1% of the available biomass (Druce *et al.* 2002a). This is less than the biomass removal on Karongwe. The biomass killed per LFU per year was also almost four times as high as on Makalali.

5.4.2 Effect of season

As was found on Makalali (Druce *et al.* 2002a), more kills were found in the hot dry season, which can most probably be attributed to prey availability and hunting conditions, as well as more favourable conditions for researchers to locate kills. The peak in October corresponds with the end of the hot dry season when the vegetation is still thin and prey is weakened after winter. During the wet season there is an influx of calves and the number of prey items killed increases. The lowest number of kills were found in April at the end of the wet season when the influx of young animals was over, and the vegetation was at its thickest, making prey location more difficult.

5.4.3 Prey selection

Other studies have shown that typically only five or so species make up between 88-95% of all kills made by lion (Stander & Albon 1993; Viljoen 1993). The top five species here (wildebeest, warthog, waterbuck, impala and zebra) are consistent with findings from other studies (Stander 1992; Mills & Biggs 1993; Funston, Mills & Biggs 2001; Power 2002a; Druce *et al.* 2002a), but only made up 72.1% of the kills recorded.

Adult kills comprised just over half of all kills located and could be due to smaller (thus young) kills not being located, but if true would be in contrast with other studies that have typically showed that 62-73% of kills are either small or young (Stander 1992; McBride 1984), although a similar study on a small reserve by Power (2002a) also showed the majority of kills (81%) were adult prey. This could have a long term detrimental effect on prey populations (Mills & Shenk 1992; Harrington *et al.* 1999; Power 2002a).

According to Radloff and Du Toit (2004) lions typically prey on proportionally much larger prey, and therefore do not compete directly with the smaller predators for most prey species. This is also shown in Hayward and Kerley (2005) who state that lions prefer medium to large prey weighing between 190 – 550 kg, and that impala are significantly not selected for by lions. Hayward and Kerley (2005) showed that gemsbok, wildebeest and giraffe were killed significantly more frequently than expected based on their availability, which was also observed on Karongwe.

Despite the fact that gemsbok, red hartebeest and eland were stocked in very low numbers (0.1 – 1% of the ungulate population), these species were represented in lion kills. It is possible that these species were preyed upon in an opportunistic manner, but it is more likely that they were actively selected for. This could be an indication that the theory of buffer species reducing predation on rarer species (Power 2002a), particularly in small reserves with small populations, is flawed, which is also shown in Hayward *et al.* (in press).

Although the lionesses killed a large number of waterbuck and wildebeest, they killed slightly more warthog, which was attributed to the fact that this smaller meal may be sufficient for females and when available is an easier prey item to capture (Funston *et al.* 2001). Such small prey could also be used by the females to teach cubs to hunt. In comparison, male lions catch more large species due to their size, food requirements and ability to pull them down. Similar to findings in Makalali (Druce *et al.* 2002a) males selected for giraffe and warthog and waterbuck were mainly fed on by females.

5.5 CONCLUSION

Although much work has been done on the feeding behaviour of lions, this study illustrated the implications of having lions on a small reserve. In conclusion, it has been shown that two pride males have a significant impact on the number of kills made as opposed to a single pride male. It is hoped that these findings will stimulate further research in similar small areas in order to broaden the understanding of lion on small reserves, and that this paper provides valuable information on the management implications of having lion on a small, enclosed reserve.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

As lion reintroductions are becoming increasingly popular in small reserves it is imperative that behavioural ecology of lions in such areas is understood. This study has illustrated the importance of rivers and drainage lines to the establishment of a lion population. It has shown that resources are the main drivers that affect home range distribution and use in male lions, although they did respond to social factors of neighbouring prides when engaging in territorial behaviour. Female lions also responded to resource factors, with particular preference for rivers, but responded more strongly to social factors from neighbouring lions by avoiding the area.

Several behaviours were altered in small reserves. Territorial behaviour was reduced, birth rate was higher, and interbirth intervals were reduced, all due to the lack of conspecific competition. From the results obtained, it is clear that a small number of lions kill a substantial number of animals every year, and can have an increased growth rate. Reserves need to ensure that the preferred prey base is large enough to sustain a lion population as well as other predators. An understanding of territorial, reproductive, and feeding behaviour in reintroduced populations can lead to enhanced management in these reserves. This information could prove valuable to other small reserves that stock lions or intend to stock lions. If a reserve is considering the reintroduction of lions the following factors need to be taken into account: (1) whether the reserve will be able to sustain the population according to the home range size required and the number of kills expected per lion per year; (2) whether a two-male coalition is necessary or if a single male will suffice; and (3) that subadults should be translocated as early as possible (between two and three years of age). These implications are important when reintroducing lions to new areas. It is hoped that this project can contribute to the general understanding of lion biology, particularly in small reserves, and aid in the conservation and management of these large carnivores.

REFERENCES

APPS, C.D. 1999. Space-use, diet demographics and topographic associations of Lynx in the Canadian Rocky Mountains: a study. *USDA Forest Service Research Papers,* pp 1-11.

BERTRAM, B. 1973. Lion population regulation. *E. Afr. Wildl. J.,* 2: 215-225.

BERTRAM, B.C.R. 1975a. Social factors influencing reproduction in wild lions. *J. Zool., Lond.,* 177: 463-482.

BERTRAM, B.C.R. 1975b. Weights and measures of lions. *E. Afr. Wildl. J.,* 13: 141-143.

BERTRAM, B.C.R. 1978. A Pride of Lions. New York: Charles Scribner & Sons.

BONATO, M. 2001. Maternal investment in captive and wild populations of lions. MSc thesis. University of Pretoria.

BRADBURY, J.W. & VEHRENCAMP, S.L. 1976. Social organisation and foraging in emballonurid bats. I. Field studies. *Behav. Ecol. Sociobiol.,* 1: 337-381.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal., 24: 346-352.*

BYGOTT, J.D., BERTRAM, B.C.R. & HANBY, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature,* 282: 839-841.

CREEL, S. & CREEL, N.M. 2002. The African wild dog: behavior, ecology, and conservation. Princeton University Press.

DRUCE, D., GENIS, H., BRAAK, J., GREATWOOD, S., DELSINK, A., KETTLES, R., HUNTER, L. & SLOTOW, R. 2002a. Prey selection of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Afr. Zool.,* 39(2): 273-284.

DRUCE, D., GENIS, H., BRAAK, J., GREATWOOD, S., DELSINK, A., KETTLES, R., PACKER, C., HUNTER, L. & SLOTOW, R. 2002b. Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe,* 47: 103-118.

FUNSTON, P.J. 1997. Review and progress report on the Northern Plains Project May 1997. Internal Report 5/97, Scientific Services, Skukuza, Kruger National Park.

FUNSTON, P.J. 1999. Predator-prey relationship between lions and large ungulates in the Kruger National Park. PhD thesis, University of Pretoria.

FUNSTON, P.J., MILLS, M.G.L., BIGGS, H.C. & RICHARDSON, P.R.K. 1998. Hunting by male lions: ecological influences and socioecological implications. *Anim. Behav.,* 56: 1333-1345.

FUNSTON, P.J., MILLS, M.G.L. & BIGGS, H.C. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool., Lond.,* 253: 419-431.

FUNSTON, P.J., MILLS, M.G.L., RICHARDSON, P.R.K. & VAN JAARSVELD, A.S. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *J. Zool., Lond.,* 259: 131-142.

FUNSTON, P.J. & JOLLEY, C.G. in prep. Management of lions (*Panthera leo*) on small game reserves in South Africa.

FUNSTON, P.J., MILLS, M.G.L. & RICHARDSON, P.R.K. In prep. Scent-marking and roaring in lions: territorial functionality and social implications. To be submitted to *Animal Behaviour*.

GETZ, W.M. & WILMERS, C.C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*., 27: 1-17.

GORMAN, M.L. & TROWBRIDGE, B.J. 1989. The role of odour in the social life of carnivores. <u>In:</u> J.L. Gittleman (ed.), Carnivore Behaviour, Ecology and Evolution. New York: Cornell University Press: 57-88.

GRINNELL, J., PACKER, C. & PUSEY, A.E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Anim. Behav.,* 49: 95-105.

GRINNELL, J. & MCCOMB, K. 1996. Maternal grouping as a defence against infanticide by males: evidence from field playback experiments on African lions. *Behavioural Ecology,* 1: 55-59.

GRINNELL, J. & MCCOMB, K. 2001. Roaring and social communication in African lions: the limitations imposed by listeners. *Anim. Behav*., 62: 93-98.

HANBY, J.P. & BYGOTT, J.D. 1987. Emigration of subadult lions. *Anim. Behav.,* 35: 161-169.

HARRINGTON, R., OWEN-SMITH, N., VILJOEN, P.C., BIGGS, H.C., MASON, D.R. & FUNSTON, P.J. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Cons.,* 90: 69-78.

HAYWARD, M.W. & KERLEY, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *J. Zool., Lond.,* 267: 309-322.

HAYWARD, M.W., O'BRIEN, J., HOFMEYR, M. & KERLEY, G.I.H. In press. Testing predictions of the prey of lion *Panthera leo* derived from modelled prey preferences. *Journal of Wildlife Management 71(5).*

HENSCHEL, J.R. & SKINNER, J.D. 1991. Territorial behaviour by a clan of spotted hyaenas *Crocuta crocuta. Ethology,* 88: 223-235.

HOOGE, P.N. 1999. Animal movement analysis ArcView extension. Biological Science Centre USGS-BRD, Alaska.

HUNTER, L.T.B. 1998. The Behavioural Ecology of Reintroduced Lions and Cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa. Ph.D. thesis, University of Pretoria.

HUNTER, L. 1999. The socio-ecology of re-introduced lions in small reserves: comparisons with established populations and the implications for management in enclosed conservation areas. Preliminary Project report, University of Natal, Durban.

HUNTER, L., SKINNER, J.D., PRETORIUS, K., CARLISLE, L.C., RICKLETON, M., WALKER, C. & SLOTOW, R. In press. Reintroducing lions *Panthera leo* to northern Kwazulu-Natal, South Africa: short-term biological and technical successes but equivocal long-term conservation. *Oryx.*

KILLIAN, P.J. & BOTHMA, J. d. P. 2003. Notes on the social dynamics and behaviour of reintroduced lions in the Welgevonden Private Game Reserve. *S. Afr. J. Wildl. Res.,* 33: 119-124.

LOW, A.B. & REBELO, A.C. 1998. Vegetation of South Africa, Lesotho and Swaziland. Dept. of environmental affairs and tourism, Pretoria.

MACDONALD, D.W. 1983. The ecology of carnivore social behaviour. *Nature,* 301: 379-383.

MCBRIDE, C.J. 1984. Age and size categories of lion prey in Chobe National Park, Botswana. *Botswana Notes and Records,* 16: 139-143.

MCCOMB, K., PUSEY, A., PACKER, C. & GRINNEL, J. 1993. Female lions can identify potentially infanticidal males from their roars. *Prac. R. Soc.Lond. B., 252: 59-64.*

MCNAB, B.K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.,* 894: 133-140.

MILLS, M.G.L. 1996. Methodological advances in capture, census, and food-habits studies of large African carnivores. In: J.L. Gittleman (ed.), *Carnivore Behaviour, Ecology and Evolution*. London: Comstock Publishing Association: 223-242.

MILLS, M.G.L. & SHENK, T.M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *J. Anim. Ecol.,* 61: 693-702.

MILLS, M.G.L. & BIGGS, H.C. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symp. Zool. Soc. Lond.,* 65: 253-268.

MIZUTANI, F. & JEWELL, P.A. 1998. Home-range and movements of leopards on a livestock ranch in Kenya. *J. Zool. Lond.,* 244: 269-286.

OGUTU, J.O. & DUBLIN, H.T. 2004. Spatial dynamics of lions and their prey along an environemental gradient. *Afr. J. Ecol.,* 42: 8-22.

ORFORD, H.J.L., PERRIN, M.R. & BERRY, H.H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). *J. Zool., Lond.,* 216: 717-733.

PACKER, C. 1986. The ecology of sociality in felids. In: D. Rubenstein & R. Wrangham (eds)., *Ecological Aspects of Social Evolution.* Princeton University Press: 429-451.

PACKER, C. 2000. Inranticide is no fallacy. *American Anthropologist,* 102: 829-857.

PACKER, C. & PUSEY, A.E. 1983a. Adaptations of female lions to infanticide by incoming males. *Am. Nat.,* 121: 91-113.

PACKER, C. & PUSEY, A.E. 1983b. Male takeovers and female reproductive parameters: a simulation of oestrus synchrony in lions (*Panthera leo*). *Anim. Behav.,* 31: 334-340.

PACKER, C. & PUSEY, A.E. 1987. Intrasexual cooperation and the sex ratio in African lions. *Am. Nat.,* 130: 636-642.

PACKER, C., HERBST, L., PUSEY, A.E., BYGOTT, J.D., HANBY, J.P., CAIRNS, S, J. & BORGERHOFF-MULDER, M. 1988. Reproductive success in lions. In: T.H. Clutton-Brock (ed.). Reproductive success. Chicago, Illinois: University of Chicago Press: 363-383.

PACKER, C, SCHEEL, D. & PUSEY, A.E. 1990. Why lions form groups: food is not enough. *Am. Nat.,* 136: 1-17.

PACKER, C. & PUSEY, A. 1997. Divided we fall: cooperation among lions. *Scientific American,* May: 32-39.

PACKER, C., HILBORN, R., MOSSER, A., KISSUE, B., BORNER, M., HOPCRAFT, G., WILMHURST, J., MDUMA, S. & SINCLAIR, A.R.E. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science,* 307: 390-393.

PEEL, M.J.S. & MONTAGU, G.P. 1999. Modelling predator-prey interactions on a Northern Province game ranch. *S. Afr. J. Wildl. Res.,* 29: 31-33.

POWER, R.J. 2002a. Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe,* 45(2): 67-75.

POWER, R.J. 2002b. Evaluating how many lions a small reserve can sustain. *S. Afr. J. Wildl. Res.,* 33(1): 3-11.

PUSEY, A.E. & PACKER, C. 1987. The evolution of sex-biased dispersal in lions. *Behavior.,* 101: 275-310.

PUSEY, A.E. & PACKER, C. 1994. Infanticide in lions: consequences and counterstrategies. In: S. Parmigiani & F. vom Saal (eds). Infanticide and parental care. Harvard Academic Publishers.

RADLOFF, F.G.T. & DU TOIT, J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *J. Anim. Ecol.,* 73: 410-423.

RUDNAI, J. 1973. Reproductive biology of lions (*Panthera leo massaica* Neumann) in Nairobi National Park. *E. Afr. Wildl. J.,* 11: 241-253.

RUTHERFORD, M.C. & WESTFALL, R.H. 2003. Biomes of Southern Africa: an objective categorisation. Pretoria: National Botanical Institute.

SEAMAN, D.E. & POWELL, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology,* 77: 2075-2085.

SCHALLER, G.B. 1972. The Serengeti lion: a study of predator-prey relations. Chicago: University of Chicago Press.

SCHEEL, D. & PACKER, C. 1991. Group hunting behaviour of lions: a search for cooperation. *Anim. Behav.,* 41: 697-709.

SCHENKEL, R. 1966. Play, exploration and territoriality in the wild lion. *Symp. Zool. Soc Lond.,* 18: 11-22.

SMUTS, G.L., HANKS, J. & WHYTE, I.J. 1978. Reproduction and social organisation of lions from the Kruger National Park. *Carnivore,* 1: 17-28.

SPONG, G. 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behav. Ecol. Sociobiol.,* 52: 303-307.

STANDER, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua,* 18: 1-9.

STANDER, P.E. 1992. Foraging dynamics of lions in a semi-arid environment. *Can. J. Zool.,* 70: 8-22.

STANDER, P.E. & ALBON, S.D. 1993. Hunting success of lions in a semi-arid environment. *Zool. Symp. Soc. Lond.,* 65: 127-141.

STARFIELD, A.M., FURNISS, P.R. & SMUTS, G.L. 1981. A model of lion population dynamics as a function of social behaviour. In: C.W. Fowler (ed.). Dynamics of large mammal populations. John Wiley & Sons: 121-134.

VAN ORSDOL, K.G. 1981. *Lion predation in Rwenzori National Park, Uganda.* PhD Thesis, University of Cambridge.

VAN ORSDOL, K.G., HANBY, J.P. & BYGOTT, J.D. 1985. Ecological correlates of lion social organisation (*Panthera leo). J. Zool., Lond.,* 206: 97-112.

VAN SCHALKWYK, A.G. 1994. Riglyne vir die bestuur van leeus *Panthera leo* in ingeperkte gebiede in Suid-Afrika. M.Sc. verhandeling (Wildbestuur), Pretoria: University of Pretoria.

VARTAN, S. 2001. Overpopulation and inbreeding in small game reserves: the lion *Panthera leo* as a case study. MSc. thesis, Percy Fitzpatrick Institute, University of Cape Town.

VILJOEN, P.C. 1993. The effects of changes in prey availability on lion predation in a large natural ecosystem in northern Botswana. *Symp. Zool. Soc. Lond.,* 65: 193-213.

WALRAVEN, F. 1989. The geology of the Pilgrim's Rest Area. Geological survey, Dept Mineral and Energy Affairs SA.

WHYTE, J. 1985. The present ecological status of the Blue Wildebeest (*Connochaetes taurinus taurinus,* Burcell, 1923) in the central district of the Kruger National Park. Partial fulfilment of the requirements for the degree of Masters of Science in the Institute of Natural Resources. University of Natal.

WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology,* 70: 164-168.

(References were cited according to the guidelines for the South African Journal of Wildlife Research).