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Abstract: Lion prey selection was studied on the Greater Makalali Conservancy (140 km<sup>2</sup>), Limpopo Province, South Africa, in order to assist with management strategies. Monitoring was carried out between February 1998 and December 2001. Lion killed 15 species, with warthog, blue wildebeest, Burchell's zebra, kudu and waterbuck constituting approximately 75% of their diet. Between 2.2% and 3.1% of the available prey biomass was killed yearly, while each female equivalent unit (FEQ) killed between 3 kg and 3.2 kg daily. Lion predation was greater for warthog, wildebeest and waterbuck and less for impala than expected. When male lion were present, a greater number of warthog and giraffe were killed, while number of females had a significant effect on medium-sized prey species and total prey species killed. Significantly more warthog, wildebeest and kudu were killed in winter than summer. More prey than expected was killed in open habitats and less than expected in thickets. Managers of small, enclosed reserves need to constantly monitor prey populations, especially medium-sized prey and may be able to reduce predation on large prey species by manipulating male lion numbers. Reserves also need to contain adequate open habitats for lion to make use of these areas for hunting.

# Prey selection by a reintroduced lion population in the Greater Makalali Conservancy, South Africa

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**Key words:** *Panthera leo*, predation, management strategies, biomass, female equivalent unit.

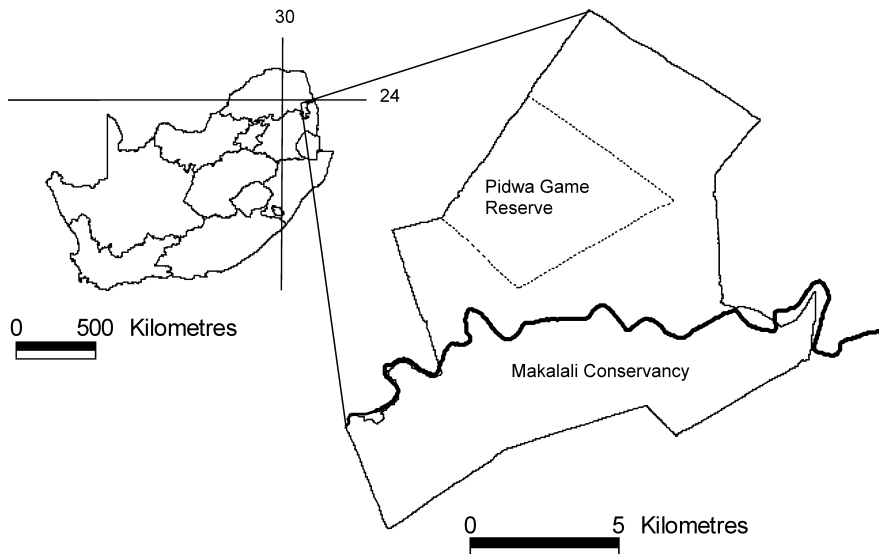
## INTRODUCTION

In recent years there has been a rapid increase in the number of small, enclosed reserves (<1000 km<sup>2</sup>) in South Africa, many of which have been established for eco-tourism and for biodiversity conservation. As these reserves are small and enclosed, almost no immigration and emigration of medium-sized to large vertebrate species can occur. Reserve managers have, therefore, had to develop management strategies that enhance the tourism potential of these reserves without jeopardizing their long-term ecological sustainability. Within these small, enclosed areas, there is potential for large predators, such as lion (*Panthera leo*) to negatively affect the prey populations. As a result, the effect of these predators on these prey populations must be monitored to ensure prey populations and diversity will be sustained.

Many studies have investigated lion foraging

behaviour in large systems such as the Ngorongoro Crater and Serengeti National Park (Hanby *et al.* 1995) in Tanzania, Manova-Gounda-St Floris National Park, Central African Republic (Ruggiero 1991), Etosha National Park (Berry 1981; Stander 1992a,b) and Chobe National Park (Viljoen 1993) in Botswana and the Kruger National Park, South Africa (Mills *et al.* 1995; Funston *et al.* 1998; Donkin 2000). However, it is only over the last few years that studies have begun to investigate lion predation in smaller, enclosed reserves. Lion predation has been shown to negatively affect general prey species in small reserves (Hunter 1998; Peel & Montagu 1999; Power 2003) and even in large reserves can have an effect on commercially important species such as roan antelope (*Hippotragus equinus*) (Harrington *et al.* 1999). As a result, introducing lion into these small systems and then leaving them without any monitoring and/or active management of the lion or prey populations could result in decreased numbers of

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**Fig. 1.** The Greater Makalali Conservancy with the Pidwa section before the fences were removed (dashed line) in October 2000. The black line through the Conservancy indicates the Makhutswi River.

certain prey species and possibly even local extinction. This is a serious concern to managers, especially when commercially important species are involved.

This study was undertaken to provide managers of the Greater Makalali Conservancy with information on the patterns of predation and foraging of the lion introduced to Makalali in order to assist them with management strategies relating to the lion and their prey species. Conclusions from this study would also assist managers of other small, enclosed game reserves where lion have been introduced. We aimed to determine (1) prey selection by the Makalali lion, (2) whether there was a difference in prey selection between male and female lion that could be used to assist managers in structuring their lion populations, (3) whether there was a seasonal difference in lion prey selection, (4) the frequency of kills and (5) whether there was a habitat difference in prey selection.

## METHODS

This study was undertaken in the Greater Makalali Conservancy, Limpopo Province, South Africa (29°09'S, 30°42'E) between February 1998 and December 2001. Makalali is situated on the Lowveld plain at an altitude of 300–500 m above sea level. The landscape is a combination of undulating terrain and rocky outcrops. Makalali is found within the savanna biome of southern Africa, with Mixed Lowveld Bushveld (Low &

Rebello 1996, Type 19) and Mopane Bushveld (Low & Rebello 1996, Type 10) as the dominant vegetation types. Makalali contains only one river, the Makhutswi River, a perennial tributary of the Olifants River. This river splits the reserve and flows from west to east. Artificial water points have been created, with some being supplied with borehole water, especially during the dry winter months.

Makalali is a relatively dry area with an average annual rainfall of 450 mm. Most of the rains fall in the summer months between October and March. Temperatures in the reserve vary from 3°C in winter to above 36°C in summer.

Makalali was established in 1993 by the initial purchase of 75 km<sup>2</sup> of cattle ranchland. It has been extended by the acquisition of adjacent farms and the cooperation of surrounding game reserve owners has led to fences being removed between neighbouring reserves, with the result that the Conservancy is now approximately 140 km<sup>2</sup> (Fig. 1). Pidwa Game Reserve was the latest property to be included in the Conservancy, when fences between Makalali and a 25 km<sup>2</sup> section of Pidwa were removed in October 2000. Large mammals that would previously have been in the area were introduced (see Appendix 1 for annual game count figures), including cheetah (*Acinonyx jubatus*) and spotted hyena (*Crocuta crocuta*). Other medium-sized to large predators that were already present in small populations on the reserve in-

cluded brown hyena (*Parahyaena brunnea*) and leopard (*Panthera pardalis*). A lion pride, which originated from the Kruger National Park, was introduced during December 1994. This group, consisting of five individuals, a mother and her four cubs (two males and two females), settled in well and after only three years the first cubs were born. Since then 35 cubs have been born, 20 of which have been translocated to other reserves. During 1999 the two pride males were removed and exchanged with two new males from Kapama Game Reserve. This was done in to introduce new genes into the Makalali pride and to prevent the males from breeding with their offspring.

#### *Population demography*

A lion database has been maintained since the lion were introduced to the Conservancy in 1994. Individuals were identified by the patterns of dots above their rows of whiskers as well as features such as facial scars and ear tears. The database lists an identity number, name, mother and father, date of birth and death, origin and location (Makalali or where they have been translocated) for each lion. Fathers were assigned to the male coalition that was present in the Conservancy during that time, while the age of the cubs and their association with lionesses, alone or in a group, were used to determine their mother.

#### *Lion kills*

Detailed lion data were collected by rangers during game drives, with some of the information being collected by researchers and other staff working on the Conservancy. Makalali is an eco-tourism destination offering game viewing as a guest activity and almost all guests request lion sightings during their stay. As a result, lion are tracked on foot if they are not on the roads. Once rangers have located the lion they return to the vehicle and drive the guests off-road into the sighting. As a result, not all of the sightings were recorded along roads (i.e. sightings were random across the reserve) and sightings were therefore, not dependant on the volume of game drive vehicles. Although there were periods when the lion were not sighted for a number of days, there was at least one sighting a day on most occasions and on one occasion nine sightings at different times were reported on one day. Lion data recorded included the date, time, individuals present, position (road and GPS), behaviour and when there was a kill, what the prey was. If the

rangers could see that the lion had made a kill, but could not identify what had been killed, then this was recorded as an unknown prey item. Although very small kills may have been missed using this method, as the entire animal including the bones may have been consumed, most kills would have been recorded as the lion were followed on their tracks and as such, areas where the lion had made kills or rested would have been seen. Spatial data relating to lion sightings and kill distribution are presented elsewhere (Druce *et al.* 2004). A large number of kills were not recorded in 1999, with the result that data from this year were left out of all of the data analysis apart from the analysis used to determine adult male prey selection and the analysis used to determine the effect of number of adult females on prey selection.

#### *Prey availability*

Aerial census counts on most prey species in Makalali are carried out each year towards the end of the dry season, when most of the tree and shrub species loose their leaves and visibility of game species from the air is the best. All aerial game counts were undertaken using a helicopter with four observers (including the pilot) and one data capturer. Transects were flown in an east/west or west/east direction and were wide enough to count individuals 150 m either side of the helicopter. All counts were started in the early morning (between 7:30 and 9:00) and all, with the exception of the 2001 game count were completed within a day. Aerial census data from 1998, 2000 and 2001 (16 September 1998, 11 September 2000 and 11–12 September 2001) were compared, using a G-test (Zar 1999), to the number of individuals of each species killed for each of the three years separately and for all three years combined.

#### *Prey selection*

All the lion kills between February 1998 and December 1998 and January 2000 to December 2001 were listed to determine the total number of kills per prey species. The percentage contribution of each prey species to the total diet of the lion was then determined.

The number of individuals of each prey species eaten was separated into the three study years. The game count numbers for each of the prey species, per year, were then used in conjunction with the total number of kills reported each year to determine an expected number of prey individuals of each species for that particular year. The actual

number of kills per prey species was then compared to the expected number for each of the study years.

As well as determining trends for each of the study years, an average game count for each of the species was determined using the game counts from each of the three years. This was then used in conjunction with the total number of individuals killed to compare the actual number of individuals of each species with the expected over the three study years. This method gave greater internal validity to the analysis, as data were an average of three years.

#### *Biomass removal*

The adult male and adult female masses, listed by Mills & Hes (1997), were used to calculate an average mass for each prey species (Appendix 1). The average mass for each species was then multiplied by the number of individuals killed each year by the lion in order to calculate the average biomass removed per lion per year, for the duration of the study period. The average mass per prey species was also multiplied by the number of individuals of each species counted during the aerial surveys for each year to determine the percentage available biomass killed by lion each year.

Biomass killed per lion per year was calculated by dividing the biomass killed each year by the female equivalent units (FEQs) for that year. An adult female was considered to have an FEQ of 1 (124.2 kg after Smuts 1980), while an adult male had an FEQ of 1.5 (Smuts 1980). Cub masses were determined using the two equations developed by Smuts *et al.* (1980) for calculating male and female cubs masses. These equations are as follows:

$$y = 4.21x + 5.29 \text{ (male cubs),}$$

$$y = 3.31x + 6.64 \text{ (female cubs),}$$

where  $y$  = mass and  $x$  = age.

Cubs were considered to be individuals under the age of two and a half years. A yearly FEQ was determined by taking into consideration the period during the year that each individual was on the Conservancy. For example, if an adult female was present on the Conservancy for six months during the year, her FEQ would be 0.5. The FEQs of cubs were determined using their age at time of removal from the Conservancy, if they were removed during the year, or their age at the end of the year.

#### *Seasonal prey selection*

The year was divided into two seasons, each of six months. The summer months refer to the beginning of November to the end of April, while the winter months refer to the beginning of May to the end of October. This division was chosen as the Conservancy receives most of its rain between November and April (summer rainfall pattern) and this is also the period when the highest temperatures are recorded. As all the kill data included the dates that the kills took place, all kills made during these six-month periods were pooled for the three years and prey selection compared between the two seasons.

#### *Adult male prey selection*

In order to determine if the presence of males at a kill influenced the prey selected, the presence of males and females at each kill were noted. We then used a *G*-test (Zar 1999) to determine if there was a significant difference between prey selected when the males were present and when they were absent.

#### *Effect of number of adult females on prey selection*

The number of adult females present at each of the kills and prey species was recorded. The maximum number of females on the Conservancy at any time was four. Adult females were taken to be those females older than three years, as lion reach sexual maturity between two and four years old (Mills & Harvey 2001). *G*-tests (Zar 1999) were then performed to determine if there was any difference in prey selected by different numbers of females.

#### *Habitat influences*

In order to determine in which habitats, if any, the Makalali lion concentrated their killing, the vegetation map of the Greater Makalali Conservancy was reduced to four habitat types, determined by their degree of openness. The nine vegetation types with their sub-communities and variants, as described by Druce (2000), were reduced to four structural habitat types. These habitats types were low closed woodland, low open woodland, low thicket and grassland.

As no vegetation description was available for Pidwa Game Reserve, only the kills that were reported before fence removal was begun (beginning of October 2000) were used. The Geoprocessing extension of ArcView was used to extract the number of kills per structural habitat type. The numbers of kills per habitat were then compared

to the expected based on the area of each habitat type within the Conservancy.

#### *Interval and distance moved between kills*

The number of days between all reported lion kills on Makalali was calculated to determine the kill frequency of the Makalali lion. This interval was independent of the individuals present at the kills to determine the kill frequency of the lion on the Conservancy rather than the feeding frequency of individual lion.

In order to determine how far the lion had to move before making another successful kill, the distance moved between kills was determined between (1) kills made on the same day and (2) kills made overnight. Analysis for the overnight kills was only carried out if a kill was recorded in the evening of one day and then the morning or evening of the following day, or if a kill was reported in the morning and then another the following morning or evening. At least some of the lion also had to be present at the consecutive kills. The Animal Movement Analysis ArcView extension (Hooge & Eichenlaub 1997) was used to determine the minimum, maximum and average distances moved between consecutive kills.

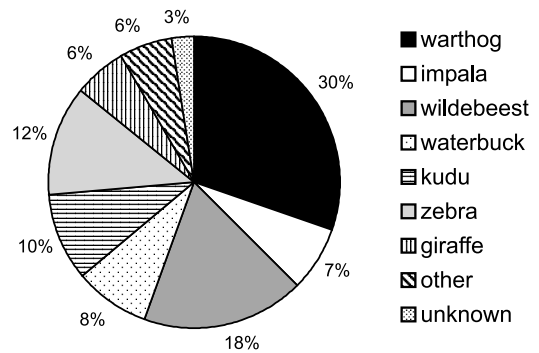
## RESULTS

### Prey selection

The lion were recorded killing 15 species on Makalali. Warthog, wildebeest and zebra contributed the greatest percentage of the lion diet (Fig. 2) and these species, together with waterbuck and kudu, made up just over 75% of their diet. There was only one record each of lion, honey badger (*Mellivora capensis*), scrub hare (*Lepus saxatilis*), steenbok (*Raphicerus campestris*) and red hartebeest (*Alcelaphus buselaphus*) being killed.

### Prey availability

The *G*-tests performed on the kill data for each of the study years indicate that there was a significant difference between the actual number of each prey species killed each year and the prey availability, based on the annual game count figures (Fig. 3). In the three study years the number of impala killed was much lower than was expected. The significant difference in 1998 ( $G_{0.05,9} = 169.676$ ,  $P < 0.001$ ) is explained by the greater number of warthog and kudu killed than expected. The greater numbers of wildebeest, waterbuck, warthog and zebra killed in 2000 than expected



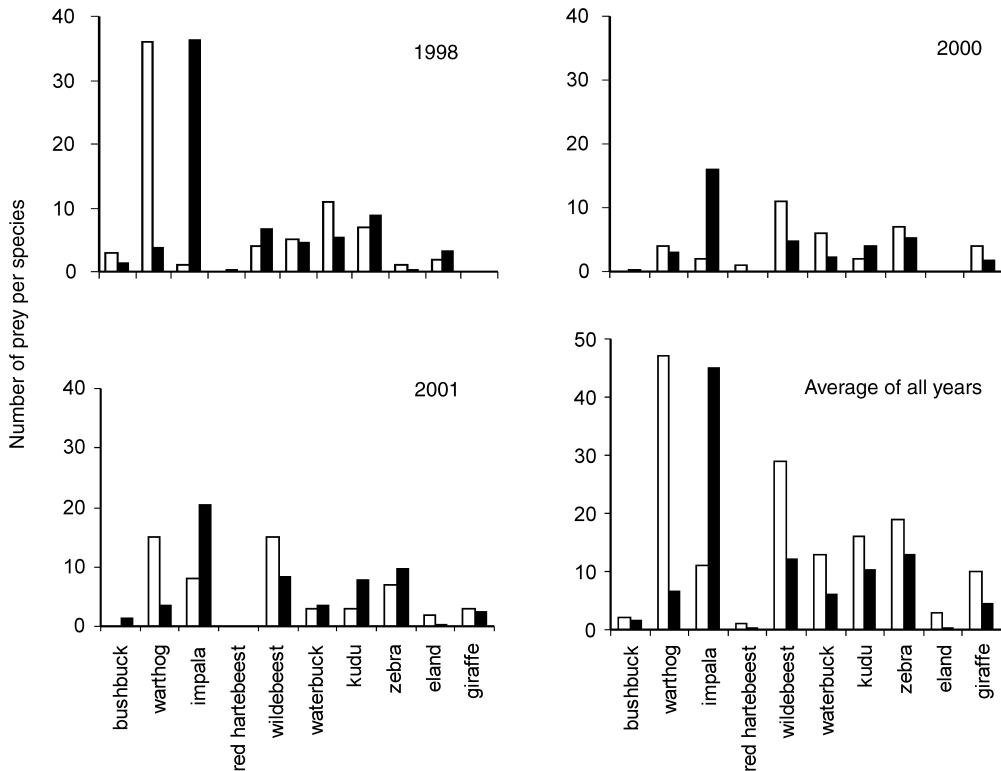
**Fig. 2.** The percentage contribution of various species to the diet of the Makalali lions. Prey falling into the 'Other' category includes all small and unusual species killed (bushbuck, common duiker, eland, honey badger, lion, red hartebeest, scrub hare and steenbok).

probably explained the significant difference observed for this year ( $G_{0.05,7} = 36.925$ ,  $P < 0.001$ ). In 2001 the major difference between the expected and actual number of kills was only observed for warthog and wildebeest. However, there was still a significant difference between the observed and the expected kills per species for that year ( $G_{0.05,7} = 45.978$ ,  $P < 0.001$ ).

The data for all of the years combined also show a significant difference between the actual number of kills per species and the expected ( $G_{0.05,9} = 283.65$ ,  $P < 0.001$ ). As with each of the three study years, impala were utilized far less than would be expected and warthog, wildebeest and waterbuck were killed more than expected. Although the results indicate that warthog were always killed more than expected, this result may not be an accurate indication of prey selection processes. Warthog are relatively small and hide in burrows and as a result are not easy to see from the air during aerial surveying. As a result, the numbers used to determine expected warthog kills might have been underestimated due to an undercount of warthog during the aerial surveys.

### Biomass removal

The Makalali lion killed between 2.2% and 3.1% of the available biomass during the study period (Table 1). The range in biomass killed per FEQ per year ranged from 1078.8 kg to 1177.8 kg, while the biomass killed per FEQ per day ranged from 3 kg in 2001 to 3.2 kg in both 1998 and 2000. These results indicate the minimum biomass removed, as there were periods where kills were not seen and therefore not recorded.



**Fig. 3.** Prey selection by Makalali lions. Actual number of kills (open bars) and the expected (solid bars) for each of the years as well as for all years combined is shown.

### Seasonal prey selection

The number of kills reported during the summer months ( $n = 51$ ) was just less than half the number of kills reported during the winter ( $n = 106$ ). Analysis of the data shows a significant difference between the number of individuals of each species killed between the summer and winter periods ( $G_{0.05,7} = 180.314$ ,  $P < 0.001$ ). The major difference between the two seasons appears to be in the much greater number of warthog, wildebeest and kudu killed during winter than summer (Fig. 4a).

### Adult male prey selection

A significant difference was demonstrated

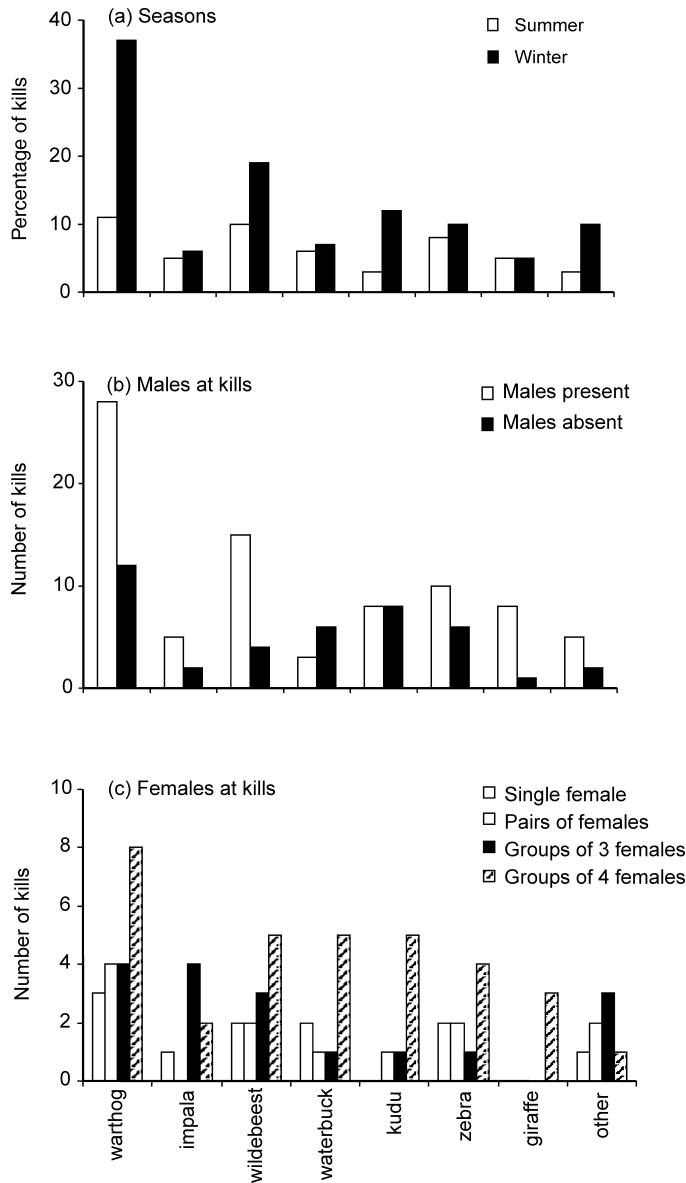
between prey species selected when males were present at a kill (in a group with females and/or sub-adults or by themselves) and when they were absent ( $G_{0.05,8} = 26.937$ ,  $P < 0.001$ ). When males were present, a larger number of warthog and giraffe were killed; however, when males were absent a larger number of waterbuck were killed (Fig. 4b).

### Effect of number of adult females on prey selection

The number of females at a kill had a significant influence on the overall number of prey species selected ( $G_{0.05,3} = 15.482$ ,  $P < 0.005$ ), with a larger

**Table 1.** Analysis of yearly biomass killed by lion on Makalali. FEQ is female equivalent unit (see text).

Year	Available biomass (kg)	Biomass killed (kg)	% Biomass killed	FEQ	Biomass killed per FEQ (kg) per year	Biomass killed per FEQ (kg) per day
1998	506 653.0	12 103.5	2.4	10.40	1163.8	3.2
2000	504 528.5	11 154.0	2.2	9.47	1177.8	3.2
2001	404 397.5	12 697.5	3.1	11.77	1078.8	3.0



**Fig. 4. a,** The effect of season on prey selection; the bars represent percent contribution of each species to all kills for the particular season. The effect of the presence of males **(b)** and female group size **(c)** on prey selection; the bars represent the actual number of each species killed.

number of most of the prey species being killed by groups of four females (Fig. 4c). However, as these results are not derived from direct observations of kills, one cannot determine whether a larger hunting group size produces a greater hunting success rate or not. Owing to a low sample size for the individual prey species, prey animals were grouped into three size classes in order to determine if female group size had an influence on the

size of prey killed. The groups were small species (<100 kg) that included steenbok, duiker, impala and warthog, medium-sized species (101–300 kg) that included red hartebeest, wildebeest, waterbuck and kudu, and large prey species (>301 kg) such as zebra, eland and giraffe. For both the small ( $G_{0.05,3} = 3.816, P > 0.25$ ) and large ( $G_{0.05,3} = 6.511, P > 0.05$ ) prey species there was no significant difference in number of kills between the different

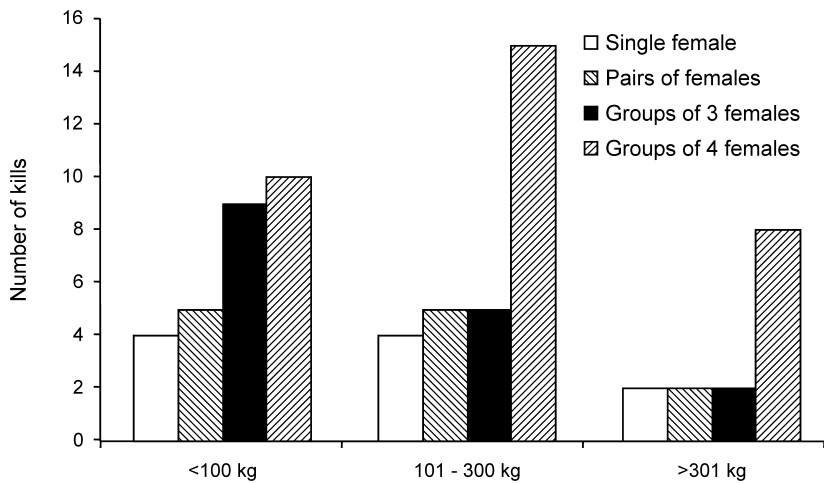


Fig. 5. The effect of female group size on prey size killed.

female lion group sizes (Fig. 5). However, the number of female lion present had a significant effect ( $G_{0.05,3} = 9.623$ ,  $P < 0.025$ ) on the number of medium-sized prey species selected, with groups of four females killing a higher number of prey species than smaller groups of females.

#### Habitat influences

There was a significant difference between the observed and expected number of kills in each habitat type ( $G_{0.05,3} = 28.33$ ,  $P < 0.05$ ). More kills than expected were observed in the low, open woodland and grassland and less than expected in the low thicket (Fig. 6). Although the greatest number of kills was reported from the low closed woodland, which constituted the greatest area of the Conservancy, the observed number of kills was very similar to the expected.

#### Interval and distance moved between kills

The average number of days between reported kills was 5.56 days ( $n = 146$  kills). The number of days between reported kills ranged from same day kills to 53 days (Fig. 7).

The average distance that the Makalali lion moved before they killed again on the same day was 3.53 km ( $n = 23$  kills). There was only one occasion where the lion killed at the same place as their previous kill. However, both prey killed in the morning and afternoon at this site were warthog. The greatest distance moved between a morning and an afternoon kill was 9.03 km.

Lion were never recorded killing at the same place on consecutive days and moved on average a distance of 3.85 km ( $n = 50$  kills) before killing

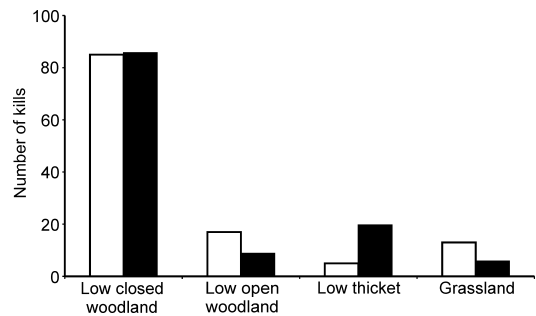
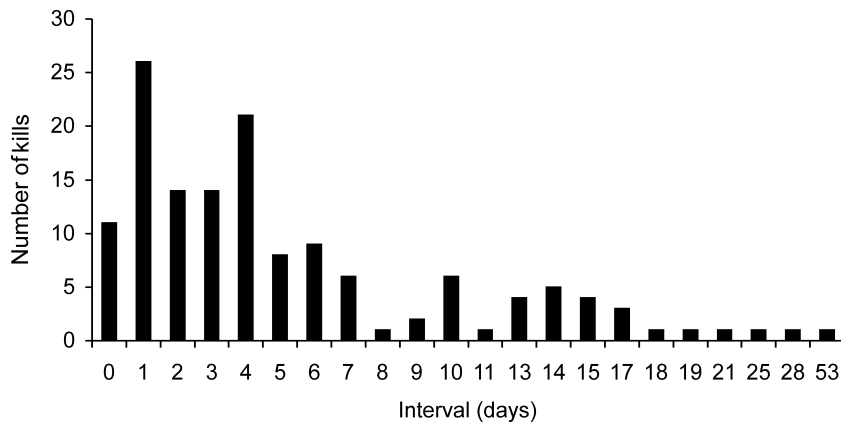


Fig. 6. Habitat influences on kill sites. There was a significant difference between the observed number of kills in each habitat type (open bars) and the expected number of kills (solid bars).

the following day. The shortest distance moved between kills on consecutive days was 0.18 km, while 9.51 km was the greatest distance moved.

## DISCUSSION

Lion have been reported to kill a wide range of species; however, it is generally less than five medium-sized to large ungulate species that constitute 75% of their diet (Schaller 1972; Rudnai 1974; Mills 1990; Hunter 1998). Warthog, wildebeest, zebra, kudu and waterbuck constituted approximately 75% of all carcasses observed in Makalali. Some early studies dealing with lion predation indicated that lion prey preference is dictated by the availability of species (Berry 1981). However, this study showed that many species, including warthog, wildebeest and waterbuck, were consistently killed with a frequency greater than would be expected based on their occurrence



**Fig. 7.** The number of days between consecutive recorded kills ranged from same day kills to 53 days.

in Makalali. Other studies have also shown that in small reserves lion tend to kill wildebeest and warthog with greater frequency than their abundance (Hunter 1998), while zebra are killed relative to their abundance (Hunter 1998). The high numbers of warthog and kudu killed by lion in 1998 could possibly be attributed to the drought experienced during 1997/1998. Warthog and kudu are very susceptible to drought and are usually the first ungulate species to lose condition, therefore becoming easy targets for predators. Although warthog are able to adapt their diet during dry periods and can dig for sub-surface plant food even in fairly hard soils (Mason 1990), they are relatively sedentary (Mason 1990) and as a result lose condition during protracted dry periods. During dry periods, the availability of browse becomes a limiting factor for kudu (Owen-Smith & Cooper 1985; Grant *et al.* 1995), with the result that kudu can also lose condition, especially in areas where they face competition from other browsers. This could also explain the selection by lion of warthog and kudu during the dry winter months.

This study has highlighted the importance of certain species to the diet of lion. Wildebeest in particular appear to be very important, especially in some small, enclosed reserves where they are relatively abundant, while warthog (Hunter 1998; this study) and kudu (this study) are generally also important prey species. Although impala were the most abundant prey species, they made up only 7% of the observed carcasses and were killed with much less frequency than would be expected based on their availability. Although some impala carcasses may have been entirely consumed and therefore not seen, this trend has also been demonstrated in other reserves such as Malilang-

we, Zimbabwe (Cotterill 1995) and in South Africa in the Phinda Resource Reserve (Hunter 1998) and the Kruger National Park (Funston 1999). In many reserves, wildebeest constitute one of the species most often killed (Berry 1981; Stander 1992a; Hunter 1998; Funston 1999; Peel & Montagu 1999). This may be as a result of wildebeest being less vigilant than smaller prey such as impala or because, unlike zebra, wildebeest generally do not manage to escape after being captured (Hunter 1998). It has also been suggested that lion will actively hunt species such as wildebeest, but that warthog are opportunistically hunted (Hunter 1998). However, in many areas warthog may be killed with a greater success rate than other smaller prey, as a result of lion trapping them in their burrows and then digging them out. This was witnessed on a number of occasions in Makalali and often involved more than one warthog being killed at a time.

Although it has been suggested that predators in a larger group or coalition are able to bring down larger prey (Kruuk 1972; Rudnai 1974; Stander 1992a; Creel & Creel 1995), female lion in Makalali tended to be more successful in larger groups when hunting all prey species and medium-sized species such as wildebeest. This matches some of the results from the plains of the Etosha National Park, Namibia, where lion were more successful in large groups when hunting all species, wildebeest and zebra (Stander 1992a). However, in contrast to Etosha, there was no significant difference between the number of kills made of large prey species (such as zebra) and the number of females. There was, however, a difference between the prey species killed when males were present at a kill and when they were absent. Studies have indi-

cated that single lionesses are able to subdue all prey species that groups of lion take, except for the largest prey species (Packer *et al.* 1990; Stander 1992b), which are often brought down by males. This would include prey such as giraffe and buffalo. Although Makalali does not have buffalo, males were present at a greater number of giraffe kills than when they were absent, indicating that their presence may be important in subduing large prey species.

Van Dyk (1997) has suggested that manipulating pride sizes in small reserves can be a valuable management technique for reducing predation on large ungulates; however, it does not appear as though this would reduce lion predation on medium-sized prey. As lion do not select for impala, the most abundant ungulate in Makalali, the abundance of medium-sized ungulates, such as impala, in reserves may not necessarily reduce predation pressure on large ungulates (Hunter 1998).

The Makalali lion ate an estimated 3–3.2 kg daily per FEQ. This is within the lower range of results from the Serengeti and Ngorongoro Crater (Hanby *et al.* 1995) and the Madjuma Lion Reserve (Power 2003), but lower than that of 5.6 kg per female per day reported from northern Botswana (Viljoen 1993). However, although there would have been some kills that were not located or recorded, especially smaller prey species, the results give a good indication of the daily consumption rate of lion in a small reserve.

A small percentage (between 2.2–3.1%) of the available biomass on Makalali was killed on a yearly basis, indicating that maintaining a pride of this size on a small, enclosed reserve is sustainable in the long term without the need to restock a wide variety of prey species. However, predation on certain highly selected prey species (in Makalali, warthog, wildebeest, zebra, kudu and waterbuck) and predation pressure by other medium-sized to large predators would also need to be considered and constantly monitored to determine if the growth rate of certain species is negatively affected through predation by either lion or other predators. This will allow managers to determine how prey populations are responding to predation pressure and whether or not certain prey population numbers need to be supplemented through the addition of more individuals.

In this study it was found that lion made more kills than expected in the more open habitat types and less than expected in the thickets. Hunter

(1998) also found that although lion may hide their cubs in thickets, they would leave their cubs and move to more open habitats to hunt. Managers, therefore, need to ensure that reserves contain large areas of the more open vegetation that will allow lion to hunt successfully in the reserve. Although the Makalali lion covered a straight-line distance of approximately 3.5 km before making another kill, this does not provide an indication as to the minimum size a reserve needs to be to satisfy all the spatial requirements of a lion pride. It does, however, provide some understanding of lion behaviour, indicating that lion do need to cover relatively extensive distances before they attempt to or are able to make another successful kill.

This study has provided a good understanding of lion feeding behaviour in a small, enclosed reserve and has highlighted the importance of studying prey selection in these reserves to ensure that both predator and prey diversity can be sustained. We conclude that, in small, enclosed reserves and in the absence of buffalo, wildebeest form one of the most important lion prey species. Many other medium-sized prey species may also be important in lion diet and it is therefore, important that numbers of these prey species are monitored and maintained in relatively high numbers in enclosed reserves in order to support lion. A number of intrinsic and extrinsic factors have also been shown to be of importance in determining lion prey selection. Intrinsic factors include the presence of males that help in capturing larger prey species. As a result managers may be able to limit numbers of large prey species being killed by reducing the number of male lion, rather than manipulating pride numbers. We also conclude that open habitat types are important for lion hunting success in small reserves and that lion need to cover distances of approximately 3.5 km before successful killing again.

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**Appendix 1.** Yearly abundance of potential prey species within the Greater Makalali Conservancy during 1998, 2000 and 2001. Data are derived from the annual aerial game counts<sup>1</sup>. Scientific names and biomass values after Mills & Hes (1997).

Common name	Scientific name	Mass (kg)	1998	2000	2001
Blue wildebeest	<i>Connochaetes taurinus</i>	215	293	346	294
Burchell's zebra	<i>Equus burchelli</i>	310	281	371	338
Bushbuck	<i>Tragelaphus scriptus</i>	37.5	54	21	47
Bushpig	<i>Potamochoerus porcus</i>	60	–	–	1
Duiker	<i>Sylvicapra grimmia</i>	19.5	13	10	5
Eland	<i>Taurotragus oryx</i>	650	14	8	6
Gemsbok	<i>Oryx gazella</i>	220	2	1	–
Giraffe	<i>Giraffa camelopardalis</i>	1010	136	121	83
Impala	<i>Aepyceros melampus</i>	50	1596	1131	713
Kudu	<i>Tragelaphus strepsiceros</i>	255	233	284	273
Mountain reedbuck	<i>Redunca fulvorufula</i>	31	–	6	–
Nyala	<i>Tragelaphus angasii</i>	87	35	22	18
Red hartebeest	<i>Alcelaphus buselaphus</i>	135	10	3	1
Sable antelope	<i>Hippotragus niger</i>	270	6	1	1
Steenbok	<i>Raphicerus campestris</i>	11	–	4	3
Warthog	<i>Phacochoerus aethiopicus</i>	68.5	167	222	121
Waterbuck	<i>Kobus ellipsiprymnus</i>	260	195	152	120

<sup>1</sup>Owing to the survey methods used, small game species are underestimated.