

Prey selection of lions *Panthera leo* in a small, enclosed reserve

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Annual trends in numbers of ungulate species on a 15 km² reserve from 1993 to 1998, were evaluated in the context of lion *Panthera leo* reintroduction during 1996, and subsequent predation by them. The ungulate prey base was enumerated annually by aerial counts and a road count that took place during 1998. The lion prey record was obtained from direct observations of a radio-located pride of eight lions and daily reserve management records. All ungulate species that underwent precipitous declines were also the most important prey to lions, comprising over 80 % of their prey, and they were preyed upon according to their availability. Lion predation was causal for the declines in wildebeest *Connochaetes taurinus*, blesbok *Damaliscus pygargus phillipsi* and warthog *Phacochoerus africana*, while the decline in kudu *Tragelaphus strepsiceros* was only partly ascribed to lions, as other non-lion related mortality sources were identified. The only ungulate species to increase subsequent to lion reintroduction was the impala *Aepyceros melampus*, which was furthermore under-selected by lions. The uncontrolled population growth of impala could have elicited ecological degradation, and it was advised to either not stock impala, or otherwise control their numbers if lions are unable to do so. Lion hunting success and kill rate, were 21 % ($n = 63$) and 1 kill/4.4 days, respectively. Three bushpigs *Potamochoerus larvatus* were killed but not utilised, and this finding is corroborated by an intensive study in Kwazulu-Natal, and this aversion is discussed. Predators can cause unprecedented declines of their prey where the prey are confined to small reserves that have no refuge from predation. On an annual basis, prey may need to be augmented to sustain predators on small reserves.

Key words: predation, predator-prey relationships, small population management, small reserves, wildlife management.

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Introduction

Predators are unable to regulate their prey where their prey populations undergo seasonal migrations of varying degrees (Sinclair *et al.* 1985; Mills & Retief 1984; Mills & Shenk 1992). However, where prey populations are resident, the predator can regulate and even limit its prey populations (Hirst 1969; Smuts 1978; Fryxell *et al.* 1988; Caughley & Sinclair 1994; Sinclair 1995; Harrington *et al.* 1999; Peel & Montagu 1999). Where the prey are at very low densities, the predator can even eliminate the prey (Fryxell *et al.* 1988). Analogous to this, enclosed reserves become islands in which

the prey are compelled to be resident, and depending on the number of predators, the prey can be regulated in the same way.

On a managed reserve of this nature, with lions *Panthera leo*, the impact that predation can have on the prey base is an important consideration (Mills 1991; Van Schalkwyk 1994; Viljoen 1996; Van Dyk 1997; Hunter 1998). To address this, one requires annual prey numbers at least, and a record of what the lions prey upon (Mills 1991; Van Schalkwyk 1994; Hunter 1998). However, to accurately and unequivocally demonstrate that a predator has had an impact on the prey; one requires additional information on the

demography of the prey populations; other non-predation related mortality sources in the dynamics of the prey populations; and how the predator selects for species, gender, age or condition (Mills 1991; Hunter 1998). This paper aimed to investigate lion prey selection in Southern Africa's smallest reserve containing free-ranging lions. This reserve was the Madjuma Lion Reserve (MLR), that was a part of the greater Mabu-la Game Reserve. The surface area size was 15 km², which was even smaller than the smallest extensively managed reserves (< 1 000 km²) that were under review by Van Schalkwyk (1994).

On fairly small reserves (40–140 km²), predators like lion and cheetah *Acinonyx jubatus*, have caused drastic declines in their preferred prey (Hunter 1998; Peel & Montagu 1999). Hunter (1998) pointed out that it remains to be seen whether predators can cause extinctions in their prey in a small reserve. Contrary to the difficulties of studying a typical African multi-predator system (Smuts 1978; Mills 1991; Bothma 1997), this reserve with one notable predator, was expected to yield a less complex understanding of a predator-prey relationship. Various aspects of predation such as hunting success, kill rates and prey species selection were examined in the light of prey abundance, and inference was to be made on the impact of this predation on prey populations.

In 1998, the MLR pride consisted of eight lions, which were borne from a reintroduced stock of three lionesses and an adult male that came from the Pilaansberg National Park (PNP). The lionesses were born in PNP, of which these lions originally hailed from Etosha National Park (ENP), and the extent to which they behave like them (Stander 1992a; 1992b; Stander & Albon 1993) would be investigated in conjunction with the main objectives. One of the females already had a litter of four cubs born at the beginning of June 1997. The sex ratio was 3:1, males to females. In May 1998, the roster was brought to 10 when two cubs were born.

Study area

Madjuma Lion Reserve is situated in the Limpopo Province, South Africa, between latitudes 24°40'–24°44'S, and longitudes 27°57'–27°59'E. The underlying geology is comprised mainly of granitic rock types, as well as sandstone and metamorphic rock, that are, in turn, overlain by six soil types (Bredenkamp & Van Rooyen 1990). The annual rainfall varies between 300 mm and 900 mm, with a mean of 602 mm per annum (South African Weather Bureau: Rooiberg station). The vegetation type of the region is Mixed Bushveld (Van Rooyen & Bredenkamp 1996), which is dominated by *Combretum apiculatum*–woodland and smaller patches of old lands grassland undergoing succession with *Cynodon dactylon* and *Cenchrus ciliaris* (Bredenkamp & Van Rooyen 1990). The only other large carnivore present is the brown hyaena *Hyaena brunnea* (Power 1998), which is not known to be an active predator, as it is mostly a scavenger (Mills 1990). The reserve contains 10 ungulate species, of which nine can be regarded as prey, and serve that purpose to varying degrees. The only function of the MLR is tourism, where rangers escort guest clientele from the Mabula Game Lodge to see the lions.

Methods

The study period during 1998 was 95 days in total (Power 1998), and that from which data was available from in 1997 was 285 days (after Jakoby 1997). During 1998, the study period spanned intermittent intervals of two weeks between March and October. During 1997, data was made available outside the researcher's study period too, hence the longer effective study period. Radio-located lions within the pride were followed in a landrover and directly observed in the same way as other workers had done (Schaller 1972; Bryden 1978; Elliot & Cowan 1978; McBride 1984; Van Orsdol 1982; 1984; Packer *et al.* 1990; Scheel & Packer 1991; Stander 1992a; b; Stander & Albon 1993; Mills & Shenk 1992; Scheel 1993; Viljoen 1993; Mills 1996; Hunter 1998; Funston *et al.* 2001). Four lions were fitted with 148 MHz radio-collars, with a 0.25 wave antennae (MK6, Telonics, Arizona). The radio signals were received by a portable receiver (Telonics, Arizona)

connected to a hand-held two-element Yagi antennae. The radio-collared individuals were members of the four different subgroups of the pride that frequently split apart from one another (Power 1998). Observations were undertaken daily in a non-random fashion, which is perceived as biased (Mills 1996), but regarded as unimportant, as the lions and their kills could be readily located and it was assumed that all prey killed during the study period could be tallied. Nocturnal observations ranged between short-duration observations up to six hours, and long-duration observations which were at least 12 hours, and were dependent on the likelihood that lions would kill (cf. Mills 1996). The adult females were the focal animals as they were regarded as the hunting lions (Van Orsdol 1982; Mills & Shenk 1992), and all their activities were observed. A Coleman spotlight (300 000 CP) was used, with an attached red-filter (Stander 1992a; Viljoen 1993) to observe the lions at night, but was switched off when the lions hunted (Mills & Shenk 1992). Observations were made with a pair of Leica 10 x 42 BA binoculars, at distances up to 400 m.

All kills were recorded, including the species, sex and age where possible. It was not always possible to gather the last two characteristics under direct observations, and where that was the case, this information was obtained from returning to the carcass the following day. Known ageing and sexing criteria were used (McBride 1984; Viljoen 1993; Bothma 1996) to assign three age-classes: adults, subadults and juveniles. The reserve management provided information on kills made from their daily monitoring. In some cases the age and sex were not recorded and hence they were assigned as unknown. Data collected from the reserve management in the previous year and that collected by researchers in 1997 (Jakoby 1997) and 1998 (Power 1998) was used, and re-analysed for this paper.

Lion hunting success was determined as the number of kills made per species, out of all hunting attempts for all prey species grouped (Van Orsdol 1984; Stander & Albon 1993; Funston *et al.* 2001). A hunt was defined according to Schaller (1972), and the outcome of a hunt ended in prey being killed or otherwise fleeing upon detecting hunting lions.

When examining prey species selection, overt selection was inferred when killed proportions of a certain species exceeded the proportions with which they occurred in, in the study area (Karanth & Sunquist 1995). The road-count numbers of the five most common ungulates, and the prey numbers killed by lions during 1998 (Power 1998) were used

to calculate the expected and observed number of prey killed respectively. The log-likelihood ratio or *G*-test statistic (Zar 1986) was used to detect prey species selection. Where a difference was found, Bonferroni simultaneous confidence intervals were proceeded to, as in other use-availability data (Neu *et al.* 1974; Byers *et al.* 1986).

The kill rate by hunting lionesses (Van Orsdol 1982; Mills & Shenk 1992) over the specified study period was determined as the total number of kills/study period (days). This was done for each species and extrapolated over a one year period.

Results

Based on the aerial census figures, the trend was for most ungulate prey populations to grow prior to lion reintroduction, and then decline subsequent to lion reintroduction. The impala *Aepyceros melampus* numbers however increased, while the warthog *Phacochoerus africanus* numbers remained relatively stable with minor fluctuations (Fig. 1).

Over the period (1997–1998), 86 lion kills were recorded (Table 1), 87 % were com-

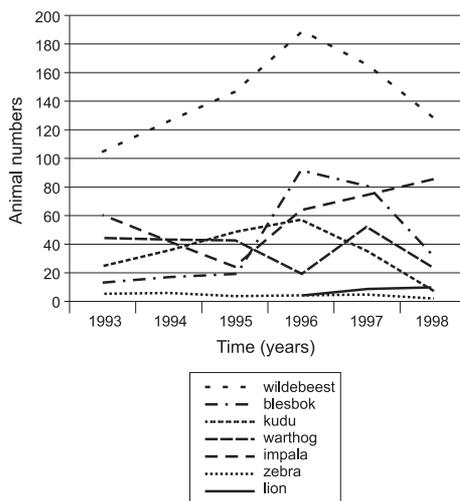


Fig. 1. Line graphs showing long-term trends in the ungulate and lion numbers of MLR since 1993. Lion reintroduction took place in 1996. The blesbok *Damaliscus pygargus philippsii* numbers were supplemented during 1996.

Table 1
 Summary of all lion kills ($n = 86$) made from March 1997 to October 1998
 which include gender and relative age characteristics of prey

Prey species	Gender									Totals
	Males			Females			Unknown			
	Adult	Subadult	Juvenile	Ad.	Subad.	Juv.	Ad.	Subad.	Juv.	
Wildebeest	13	2		12					4	31
Blesbok	5			6			2		1	14
Kudu	8	3								11
Warthog	4			9			1		4	18
Impala	1			1	1					3
Bushpig							3			3
Genet							1			1
Porcupine							1			1
Aardvark							1	1		2
Ostrich				2						2

Table 2
 Summary of total mortality percentages of five ungulates on MLR, inclusive of all lion kills
 and other mortality sources and the annual kill rate

Prey species	% lion kills in 1998 ($n = 30$)	% lion kills in 1997 ($n = 55$)	Other non-lion related mortality (1997), as % of total mortality	Per annum kill rate
Wildebeest	40.0	36.4	16.7 ($n = 24$)	30.7
Blesbok	10.0	18.2	9.1 ($n = 11$)	13.5
Kudu	16.7	10.9	72.7 ($n = 22$)	10.6
Warthog	20.0	20.0	0 ($n = 11$)	13.6
Impala	0.0	5.4	0 ($n = 3$)	2.8

prised of four ungulate species, and 93 % were prey between 50 and 300 kg. Wildebeest *Connochaetes taurinus* comprised 37 %, warthog 21 %, kudu *Tragelaphus strepsiceros* 13 %, and blesbok 16 %. A small spotted genet *Genetta genetta* and three bushpigs *Potamochoerus larvatus* were not utilised. The one bushpig was though partially eaten, but the lions regurgitated the meat subsequently. Anomalous prey like porcupine *Hystrix africae australis*, aardvark *Orycteropus afer* and ostrich *Struthio camelus* were also recorded.

Male individuals comprised 55 % ($n = 66$) of kills where gender was known, while adults comprised 81 % of all prey, while younger

individuals (subadults & juveniles) made up the remainder (Table 1).

There were a total of 63 hunts observed, of which 13 were successful. Therefore hunting success was 21 % for all prey species. The kill rate was one kill every 4.4 days, implying that 83 kills were made annually, regardless of whether they were utilised or not. The annual off-take by lions for the prey animals was calculated (Table 2). Other non-lion related mortality (Table 2) sources included fence electrification, old age, and various unidentified sources, which could have included food shortages. Excluding the small recruitment of the year for each species (Madjuma census figures 1997), the calculat-

Table 3

Prey species selection by lions in the MLR based on the 1998 road count and kill record, using Bonferroni simultaneous confidence intervals. P_o = observed use proportion, P_{io} = expected use proportion, n = kill sample, total $Z = 2.34$, Selection status: -ve = avoidance, +ve = overt selection, 0 = selection in accordance with numbers

Prey species (1998 road counts)	P_o	P_{io}	n	Bonferroni intervals	Selection status
Wildebeest	0.460	0.44	12	$-0.06 < P_{io} < 0.98$	0
Blesbok	0.115	0.104	3	$-0.22 < P_{io} < 0.45$	0
Kudu	0.192	0.061	5	$-0.02 < P_{io} < 0.37$	0
Warthog	0.231	0.100	6	$-0.21 < P_{io} < 0.67$	0
Impala	0.000	0.288	0	$-0.2 < P_{io} < 0.20$	-ve

ed per annum kill rate does conform to the same number at which ungulate populations declined by (Table 2) suggesting that predation over-rode the net growth rate

There was an overall significant degree of prey species selection by the MLR lions from the road count data ($G = 47$, $df = 4$, $p < 0.001$). Owing to this, it was decided to proceed to construct Bonferroni confidence intervals and further analyse this claim. It was found that the MLR lions appeared to prey on four ungulate prey species according to their numbers in the populations, and impala were significantly under-utilised (Table 3).

Discussion

As predicted by predation theory (Caughley & Sinclair 1994), small resident prey populations, when subject to predation, without refuge from predators, or where migration is inhibited (fencing), can undergo significant declines (Fryxell *et al.* 1988; Mills 1991; Sinclair 1995; Hunter 1998; Peel & Montagu 1999). At MLR, the four ungulate species that underwent dramatic declines, were also the most important prey to lions, comprising over 80 % of lion kills. It was imminent that some ungulate populations could have become extinct within a year (Fig. 1), which remains to be seen on a small reserve, as Hunter (1998) pointed out. In identifying the cause of prey declines, it is imperative to also account for other sources of mortality,

other than predation (Mills 1991; Hunter 1998), and accordingly, all non-lion related mortality was recorded for the MLR (Table 2). For wildebeest and blesbok, non-lion related mortality accounted for a small fraction ($< 17\%$) of total mortality, and in warthogs no other source of mortality could be identified other than lion predation (Table 2). However, in the case of kudu, non-lion related mortality was much greater ($> 70\%$) than that contributed by predation *per se*. It is thus argued that lion predation was the main cause of population declines in wildebeest, blesbok and warthog, while predation might have had a secondary role in hastening the decline in the kudu population. In kudu, mortality is often associated with dry season food shortages (Owen-Smith 1984) and the consequences of dimorphism in the long-term, particularly in adult males, which may be further exacerbated by predation (Owen-Smith 1993).

Lion predation was aimed at the adult segment of ungulate populations, moreover juvenile predation, which is most certainly because the 1998 study period (Power 1998), fell outside the main ungulate seasonal birth peak. Alternatively, the study methodology could have been the reason. Prey like warthogs and juvenile ungulates are rapidly consumed (8 min for juvenile warthog: Power 1998) and a study of this nature might have overlooked the fraction of smaller prey (Mills 1996). Elsewhere, higher juvenile predation by lions was reported, which was pre-

sumably because of the continuous presence of observers with study lions (McBride 1984; Viljoen 1993; Stander 1992a). Notwithstanding, if adult mortality was important at MLR, it could have been a contributor to the observed population declines, as lion predation was simulated to have the greatest impact in the KNP when the adult segment of the zebra (Mills & Shenk 1992) and roan (Harrington *et al.* 1999) populations were preyed upon.

The MLR lions favoured wildebeest, warthog and kudu as prey, like they do in savannas elsewhere (Mills 1991), that was in accordance with their numbers (Table 3). This would however be the first published record of blesbok as lion prey, as lions have been eliminated from the blesbok's distribution range, though this species is non-native to the Limpopo Province bushveld (Skinner & Smithers 1990). The absence of zebra predation was a reflection of their numbers, and it is suggested that they should be stocked on account of them being an important prey species (Pienaar 1969; Whateley & Brooks 1985; Mills 1991; Mills & Shenk 1992; Mills & Shenk 1992; Scheel 1993; Stander & Albon 1993; Viljoen 1993; Funston *et al.* 2001). The fact that bushpig were not utilised, and when so, regurgitation took place can be corroborated with the findings of Hunter (1998) at Phinda. He reported 10 out of 13 bushpig kills that were abandoned and only partially fed upon (Hunter 1998). Boma-contained lions have also been known to show disdain to eating bushpig meat (Van Dyk *pers. comm.*). Two reasons are put forward why this could be so. Firstly, bushpig might have glandular secretions that may impart some distastefulness to the flesh, which would be to the disdain of the eater and explain why lions regurgitate this once eating. Secondly, lions could be construed as 'finicky' carnivores that feed only on true herbivores on the appropriate secondary trophic level. The bushpig is more omnivorous than the warthog (Skinner & Smithers 1990), and it could be likened to another carnivore, which is infrequently preyed upon (*cf.* leopards). However, nutritionally-stressed lions, or any other predator for that

matter, would not have an aversion to feeding on non-herbivore prey (Griffiths 1975; Eloff 1984; Mills 1984; Skinner & Smithers 1990). This phenomenon has largely been overlooked as bushpig are either rare or absent from many of the sites where lions have been intensively studied. Only a fully-fledged research study on the myochemistry of bushpig meat could properly elucidate this answer.

The MLR hunting success is intermediary between that reported for ENP (15 %: Stander & Albon 1993) and other areas such as the R'wenzori National Park (28.9 %: Van Orsdol 1984). Hunting success was highest on dark moonless nights (Power 1998), which is due to the lessened ability of prey in detecting hunting lions (Van Orsdol 1984; Stander & Albon 1993; Funston *et al.* 2001). Contrary to ENP lions (Standar & Albon 1993), MLR lions had exercised some diurnal hunting with fairly high success (Power 1998), which is perhaps because of the closed nature of vegetation (Funston *et al.* 2001), and the availability of diurnal warthog, which are a main contributor to diurnal hunting success in lions (Van Orsdol 1984). The extent to which the MLR lions hunted with a coordinated strategy of ENP lions (Standar 1992b), could not be properly ascertained owing to the conditions of the vegetation and darkness. For those that were witnessed ($n = 6$) during daylight, the largest lioness consistently occupied a central position in all hunting, whilst the two smaller lionesses were wings that encircled the prey as described by Stander (1992b).

A kill rate of seven wildebeest per killing lioness per annum for KNP (Mills & Shenk 1992; Funston 1999) is lower than the 10.2 wildebeest per lioness per year for MLR, which is perhaps because of the limitations in prey switching on MLR when compared to the more diverse KNP prey base. MLR lions exhibited no significant selection for any species, except for impala. Non-selective predation patterns occur where large prey are scarce (Karanth & Sunquist 1995), and where prey choice is seemingly limiting (Griffiths 1975). At Phinda, wildebeest were

preyed upon at three times their availability, warthogs twice, and kudu at their availability, while impala were under-selected (Hunter 1998) like the MLR. It appears that impala are more frequently preyed upon in larger reserves (Bryden 1978; Whateley & Brooks 1985; Mills & Biggs 1993; Funston *et al.* 2001), and the fact that they were significantly under-represented in the diet of MLR lions, might be ascribed to the extreme alertness and superior vigilance behaviour of this species (see Mooring 1999). At Phinda, impala underwent a 200 % increase in vigilance (measured as the proportion of individuals being vigilant) following felid reintroduction (Hunter & Skinner 1997), which suggests that the slightly higher predation upon them during 1997 (Jakoby 1997), was because impala were more naïve to the presence of lion. With a constrained and below average pride range size (ca. 15 km²), it is contended that the encounter rate with impala would be much higher than it would be in a larger reserve. In larger reserves, then, larger lion prides frequently range out of the ranges of impala, and the impala thus have a reprieve in awareness for lions. With the higher predator-prey encounter rates experienced on smaller reserves, it could be the primer to 'fine-tune' their senses to a familiar predator. It is hypothesised then that impala will feature less in the diet of lions when their pride ranges are small, whether this is because of confinement or ecological reasons. Since impala were infrequently preyed upon they would not be serving their purpose as prey. Despite this, what is more at stake, though, is that an ever increasing abundance of impala could severely impact upon the vegetation and other herbivore habitats. Impala are highly-selective mixed feeders (Fairall & Klein 1984; Du Toit 1988; Skinner & Smithers 1990), that have the ability to denude the amount and change the composition of the herbaceous layer to the detriment of other herbivores (Wentzel *et al.* 1991), and reduce predator stalk cover (Power 1998), which is an important variable influencing hunting success (Kruuk 1986; Sunquist & Sunquist 1989; Van Orsdol 1984; Funston *et al.* 2001). Following this,

for ecological reasons, managers should closely monitor impala numbers, and intervene to control impala numbers if lions are unable to do so. Impala appear to successfully utilise a habitat that can be construed as 'enemy-free space' (Jeffries & Lawton 1984; Begon *et al.* 1996), which would not be favoured by potentially competing herbivores (Wentzel *et al.* 1991), or otherwise not conducive to the hunting antics of lions, owing to the reduction in stalk cover (Van Orsdol 1984), which is typical of impala habitat (Wentzel *et al.* 1991).

Prey like wildebeest, kudu, warthog, zebra and blesbok would serve effective buffer prey species, if there is a desire to safeguard rare or expensive ungulate populations. Wildebeest are especially a favoured prey species, and lions are known to have a great impact on their populations in both large and small reserves (Mills & Shenk 1992; Mills & Biggs 1993; Hunter 1998; Peel & Montagu 1999). On small reserves (< 2 000 ha) managers might be compelled to restock reserves with prey or otherwise increase area size through the conservancy approach, and if that is not an option, to not liberally stock small reserves with lions. Large protected areas that create prey confinement by water provisioning can be prone to prey declines by predators (Kruuk 1986; Young 1992; Hunter 1998; Harrington *et al.* 1999), in the same way that small enclosed reserves would. In managing an assemblage of predators on a reserve, it can be expected that similar prey declines of the same species will occur, and the real challenge is to accommodate this. Research would need to be aimed at sustainability of reserves for predators, but in the meantime the suggested practice is to have to re-supplement prey populations on small reserves.

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