

CHAPTER 6.

FEEDING ECOLOGY AND PATTERNS OF PREDATION BY REINTRODUCED LIONS AND CHEETAHS.

As conspicuous, locally abundant major predators, the feeding ecology of lions and cheetahs has received considerable attention in the scientific literature. The majority of studies of both species have focused on their diet, feeding behaviour, hunting patterns and foraging dynamics (Mitchell *et al*, 1965; Makacha & Schaller, 1969; Pienaar, 1969; Schaller, 1972; Eloff, 1973; Eaton, 1970, 1974; Rudnai, 1974; Bertram, 1978; Burney, 1980; van Ordsol, 1982, 1984; Smuts, 1982; Mills, 1984; Packer & Ruttan, 1988; Ruggiero, 1991, Stander, 1990, 1992; Scheel, 1993; Viljoen, 1993; Packer *et al*, 1990, 1995). Recently, comprehensive studies such as those by Caro (1994) on cheetahs, and Packer and co-workers on lions (Packer & Ruttan, 1988; Packer *et al*, 1990, 1995) have examined such patterns in terms of the sociality of lions and cheetahs. More than any other felids and indeed most other large carnivores, the relationship between lion and cheetah feeding habits and other critical aspects of their behaviour and ecology are beginning to be well-understood.

The social systems of lions and cheetahs furnish both advantages and disadvantages in terms of feeding ecology, which in turn may influence some aspects of sociality. Reasons for the formation of prides by lions were long attributed to the benefits group hunting conferred by being able to subdue and kill large, dangerous prey (Wright, 1960; Schaller 1972, Rudnai 1974; Kruuk, 1975, Wilson, 1975; Elliot & Cohen, 1977; Bertram, 1983). However, research by Packer and co-workers (Packer & Ruttan, 1988; Packer *et al*, 1990) has demonstrated that, while increased pride size does yield some foraging benefits, other complex factors such as the defence of young, the enhancement of reproductive success and the maintenance of long-term territories contribute to patterns of lion sociality. Concomitantly, this has implications for their feeding ecology.

Similarly, the unusually variable system of cheetah sociality in which females are always solitary, and males may form coalitions or may remain alone (Caro, 1994) presents costs and benefits. Even the largest aggregation of cheetahs could probably not tackle the very large ungulates such as buffaloes and giraffes where group size in lions plays a significantly beneficial role (Packer *et al*, 1990). However, male cheetahs in coalitions can tackle larger animals than do single males or females, and hunting larger prey is one adaptation used by male cheetahs to meet the increased (collective) energetic demands of group living (Caro, 1994).

Various aspects of lion and cheetah ecology which may influence their patterns of predation and foraging differed markedly at Phinda compared to most other well-studied populations. First, reintroduced felids were faced with a high density and diversity of naïve prey species which had experienced low predation pressure prior to reintroduction (Chapter 8). Furthermore, the ungulate fauna in the reserve was dominated by small to medium-sized species such as impalas and nyalas. Thirdly, there were no resident lions and cheetahs present and numbers of other major predators, particularly leopards and spotted hyaenas were low due to historical persecution. Accordingly competition for food resources was low. Additionally, some aspects of lion and cheetah population dynamics were unusual compared to established populations (Chapter 5). Lions prides were generally small so that competition for food within prides was low. Also, the period of the study spanned a period when prides grew considerably, starting when small prides were released and ending when prides were reaching the sizes of those elsewhere. This presented an opportunity to examine changes in prey selection related to increasing group size over time. Finally, for cheetahs, the fact that the survival rate of cubs was high placed different foraging pressure on females compared to other well-studied populations where the survival rate of cubs may be very low. Moreover, patterns of predation for cheetahs are generally only well-known from very open habitat such as the population of the Serengeti plains. The *Acacia*-dominated woodland mosaic at Phinda presented an opportunity to examine cheetah feeding ecology in a very different environment to the 'classic' grassland habitat of cheetahs.

In this chapter, I examine lion and cheetah feeding ecology under these circumstances. Specifically, I explore the following questions:

- 1: Does lion foraging behaviour reflect the reduced requirements inherent in small pride size, and the abundance of smaller, easier-to-kill prey species at Phinda?
- 2: Does this behaviour change over time as pride size increased due to rapid reproduction and high survival of cubs?
3. What are the patterns of feeding ecology of cheetahs in woodland-dominated vegetation and can cheetahs successfully forage in habitats often assumed to be sub-optimal?
- 4: Does the high rate of survival of cheetah cubs place increased demands on mother cheetahs and if so, how do they respond?

Finally I also examine the importance of food resources for reintroduced carnivores in terms of project success and emphasise some management issues related to predator-prey interactions following carnivore reintroduction.

METHODS.

I collected data on feeding ecology by three means. First, where possible I followed hunting felids for extended periods to observe kills as they were made. I usually followed at the greatest distance which enabled me to maintain contact with the cats but also so as not to interfere with the hunt. In open regions, this distance was up to 300m but in woodland it was often reduced to 40-50m. For lions which did most of their hunting at night, I used a spotlight (as detailed in Chapter 2) which I switched off when they encountered prey and waited until the attempt had been made before locating them again. Following cats for extended periods had limited applicability at Phinda due to areas of dense vegetation where I could not drive. When I lost cats in dense bush, I moved ahead of them in their path of travel to areas of open habitat to wait for them to emerge, checking their progress by the radio-signal. If they did not emerge and remained stationary for some time, this often indicated they had killed. I determined the location by triangulation and attempted to walk into the site once cats had left, usually the following morning. In this way I frequently found fresh kill remains.

I often located cats which had already made a kill which, I have termed a radio-location observation (after Mills, 1992). For each sighting of cats with a carcass, I recorded whether it was killed by the cats feeding on it, scavenged by them, or origin unknown. To assess origin of carcasses, I relied as much as possible on direct observation but other clues assisted identification. Old carcasses were readily identified by their level of decomposition and I recorded these as scavenged. Fresh kills, even when they were not witnessed could sometimes be identified by signs of the capture or hunt (such as tracks or signs of struggle in sandy soil), where dead ungulates had fresh blood flowing from bite wounds to the neck or had fresh vegetation in their mouths. If the kill had not been witnessed (or heard), or I could not find evidence of this type, I recorded the carcass origin as unknown.

Finally rangers on game drives provided many direct observations of kills and carcasses. I usually checked their reports (which I generally received as they occurred via radio) by visiting the site to confirm details of the kill. All rangers were proficient in species identification and generally provided good information on sex and age of prey species. For the latter parameter, I provided guidelines according to my categories (see below), but recorded it as unknown unless I was able to confirm it myself or had consensus from two or more rangers at the same sighting.

For all kills, I recorded the species, sex (where possible), age (juvenile, sub-adult, adult: where possible), the time of the kill if known, the location and the surrounding habitat type. I also identified and recorded all cats which were present at the carcass.

Where I knew the time the kill had been made, I recorded how long felids spent feeding on the kill before abandoning it. I also made an estimate of the weight of the kill based on published data of herbivore age-sex classes¹.

I also recorded occasions when cats had obviously fed but I could not locate the kill: these sightings I recorded as 'unobserved kills.' To attempt some estimation of the prey type of unobserved kills, I scored the belly size of cats after feeding on different prey species on a five-point scale where one was 'quarter-full' (the lower limit when it was obvious to me that cats had fed) and five was gorged. I derived a reference list of likely prey fed upon for unobserved kills based on belly size which took into account the number of cats feeding and the prey species, age-class and sex. For example, a coalition of three male cheetahs with a belly size of five had probably consumed an animal approximately the size of the maximum prey weight normally taken, which at Phinda was an adult male nyala (or thereabouts). This method is clearly biased towards larger kills, particularly for lions which often did not show any visible evidence of feeding on small and medium-sized species, depending on the size of the pride. Accordingly, I do not make any attempt to accurately identify unobserved kills and present this data in coarse categories: small, medium and large kills. Any attempt to refine prey identification of missed kills based on belly size would be questionable. Nonetheless, I was reasonably confident of my estimations particularly given that I located most cats daily and could accurately assess if they had fed since my previous sighting.

Statistical analyses

To assess whether lions and cheetahs were selecting certain prey, I used Chi-squared tests which compared availability of prey species (i.e. the relative frequency at which they occurred in Phinda) to the rate at which they were killed by lions and cheetahs. Herbivore population estimates and demographic characteristics were established for eight common ungulates at Phinda by seasonal censuses, which I detail in the following chapter. I also compared population structure of eight herbivore species with the frequency of different sex-age classes to determine if selection for any cohort was occurring. For all the analyses I excluded scavenged carcasses as well those species which were killed and left uneaten, which occurred frequently for lions with other carnivores, reptiles and so on. This never happened with cheetahs, though I have excluded two male cheetahs which were killed in territorial clashes and later fed upon (Hunter & Skinner, 1995; Appendix III).

¹ Weights of ungulates after the following sources: Anderson, 1978 (nyala); Attwell, 1977 (wildebeest); Fairall & Braack, 1976 (impala); Hall-Martin, 1976 (giraffe); Mason, 1985 (warthog);

To examine if prey selection was related to increases in group size in lions and cheetahs (females with cubs) I calculated the total number of individuals (of either lions or cheetahs) at each kill in terms of biomass expressed as Female Equivalent Units (FEQs). FEQs have been used as an estimate of carnivore biomass in previous predator-prey studies, particularly of lions (Bertram 1979, Packer *et al* 1994). However, calculation of FEQs has tended to be crude: for example, Bertram (1979) used general estimates where cubs weighed 1/9th of adult female weight during the first third of a year of life, 2/3rds in the second third of a year of their life and so on. I had very accurate estimates of dates when cubs were born, so I knew ages of all cubs (Chapter 5). I used regression equations relating mass to known age to calculate FEQs for all cubs at every kill. For lions, I adopted the following equations from Smuts (1980) which he derived separately for male and female lions from a sample of 158 males and 186 females; $y = \text{mass}$, $x = \text{age}$:

$$y = 4.21x + 5.29 \text{ (males).}$$

$$y = 3.31x + 6.64 \text{ (females).}$$

Equivalent data do not exist for cheetahs in the literature so I derived a growth equation irrespective of sex from mass data in Laurenson (1993: 79 free-living cubs from the Serengeti, aged 6-48 days old) and unpublished data provided by Marker² (112 free-living cheetahs from Namibia aged 3-24 months). This is presented in Figure 37. This is less than ideal for two reasons: east African cheetahs may be slightly smaller than southern African individuals (Caro 1994: 382) and Marker's data is based on estimated, rather than known, ages of animals. Nonetheless, better data for wild cheetahs do not exist and these disadvantages are probably insignificant for their use here.

For every cub at every sighting with a kill, I estimated mass from its known age according to the regression equations and then divided this by mean female weight to give the FEQ. Mean lioness weight was taken as 124.2kg (Smuts, 1980) and mean female cheetah weight was 36.7kg (Marker; unpubl data: 37 females, range 25.5 - 50.5kgs). An adult female's FEQ was 1.0 and the total FEQ for each kill was calculated by tallying the FEQs of the cubs with that of the female's. If males were present, I included their FEQ as 1.5 for lions which average 50% heavier than lionesses (Smuts, 1980). Adult male cheetahs are very rarely in attendance to a mother with cubs when she makes a kill and are unlikely to be a factor in any prey selection by female cheetahs that may be occurring. Accordingly, I excluded three cases when male cheetahs accompanied a mother when she killed. Therefore, for lions on kills in this study, FEQ ranged between 1.0 (single female) to 7.97

Schmidt, 1984 (common duiker); Silva & Dowling, 1995 (reedbuck); Skinner & Smithers, 1990 (blesbok, kudu, red duiker, steenbok, suni); Smuts, 1974 (zebra); Wilson, 1970 (kudu).

² Marker, L. Cheetah Conservation Fund, PO Box 247 Windhoek, Namibia, Tel +264 658 11812

(pride of 3 females with cubs of different ages) and for cheetahs, the range was 1.0 (single female) to 4.35 for a female with five 13mo cubs.

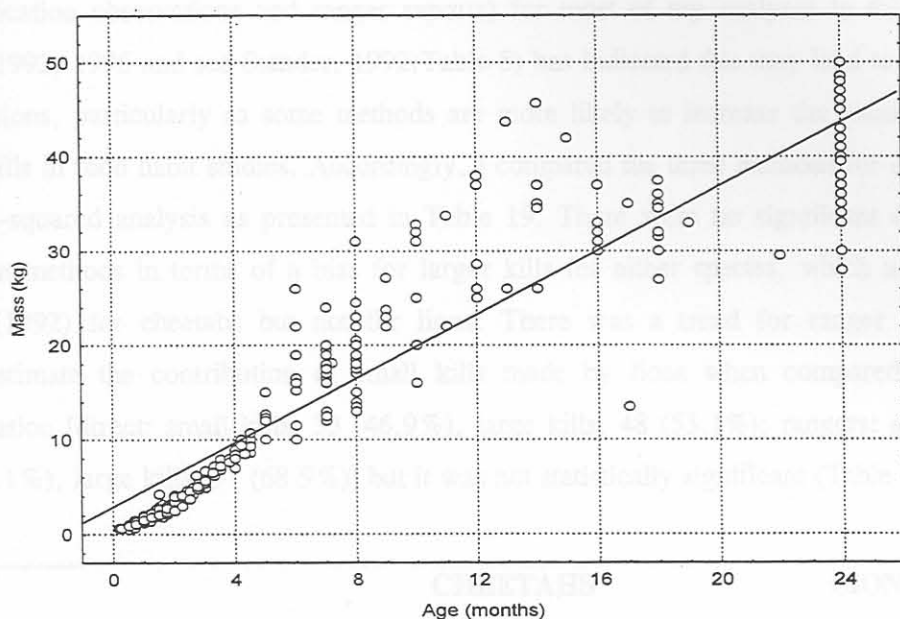


Figure 37: Cheetah growth rate for calculating FEQs. Scatter diagram and least-squares regression line showing relationship between body mass and age. $y = 2.928 + 1.697x$, $r^2 = 0.8470$, $n = 191$. Data from Laurenson (1993) and unpublished data provided by Marker¹, details in text.

I used single regression analyses to determine if selection of larger prey species was related to increasing group size as measured by FEQs. The independent variable was FEQ and the dependent variable was the weight of prey. However, much of my data on kills were gathered by methods which bias data towards larger kills (see above). Consequently, I needed to ensure that the relative likelihood of finding small kills versus large kills did not decrease with increasing FEQs (due, for example, to increased competition between individuals in groups of larger FEQs). Therefore, to establish the rates at which carcasses were utilised by different sized groups, I calculated the average time spent per cat on kills of different weights for different FEQs. I used a Kruskal-Wallis ANOVA to test if this differed for different group sizes. I performed this analysis separately for lions and cheetahs.

RESULTS

General patterns of predation.

I have combined data from all three methods of data collection (direct observation, radio-location observations and ranger reports) for most of my analyses in this chapter. Mills (1992, 1996 and see Stander, 1992:Table 8) has indicated this may lead to erroneous conclusions, particularly as some methods are more likely to increase the contribution of large kills in food habit studies. Accordingly, I compared the three methods for differences by Chi-squared analysis as presented in Table 19. There were no significant differences between methods in terms of a bias for larger kills for either species, which agrees with Mills (1992) for cheetahs but not for lions. There was a trend for ranger reports to underestimate the contribution of small kills made by lions when compared to direct observation [direct: small kills, 33 (46.9%), large kills, 48 (53.1%); rangers: small kills, 41 (31.1%), large kills, 91 (68.9%)] but it was not statistically significant (Table 19).

	CHEETAHS	LIONS
Direct vs radio-location.	$\chi^2 = 0.614, p < 0.433, df = 1$	$\chi^2 = 1.096, p < 0.295, df = 1$
Direct vs ranger reports.	$\chi^2 = 0.265, p < 0.606, df = 1$	$\chi^2 = 3.505, p < 0.061, df = 1$
Radio location vs ranger reports.	$\chi^2 = 1.590, p < 0.207, df = 1$	$\chi^2 = 0.627, p < 0.428, df = 1$

Table 19. Results of chi-squared analysis comparing occurrence of large vs small kills for three methods of data collection on lion and cheetah feeding ecology. Following Mills (1992), large kills were >25kg for cheetahs and >100kg for lions.

Lions killed 28 species and cheetahs killed 15 species at Phinda (Table 20). 97.8% and 99.7% of lion and cheetah kills respectively were mammals. Lions generally abandoned prey without eating it when the species were other carnivores (mustelids, herpestids and three cheetahs), reptiles and one wattled plover caught by an 8 month old cub. In nine cases, they killed and abandoned bushpigs without feeding, apparently without reason. Cheetahs always ate from all species they killed. Cannibalism occurred in one case for lions (three neonates eaten) and two cases for cheetahs (Hunter & Skinner, 1995; Appendix III).

Prey species	Cheetah	Edible biomass**	Lion	Edible biomass**	Total
Mammals					
aardvark			2	90 (<1.0)	2
blesbok [#]	1	27 (<1.0)	1	54.9 (<1.0)	2
bushbuck	1	22.5 (<1.0)			1
bushpig			13 [*]	90.5 (<1.0)	13
cane rat, greater			2	8.0 (<1.0)	2
cheetah	2 [‡]		3 [*]		5
domestic cow [#]			2	636.5 (1.8)	2
duiker, common	15	204.5 (1.7)	4	49.1 (<1.0)	19
duiker, red	8	81.0 (<1.0)	6	64.8 (<1.0)	14
giraffe	2	147.5 (1.2)	8	1858.0 (5.1)	10
impala	112	2876.4 (23.8)	20	650.7 (1.8)	132
kudu	5	300.0 (2.5)	14	1774.4 (4.8)	19
lion			5 [§]		5
mongoose, banded			3 [†]		3
mongoose, white-tailed			3 [*]		3
nyala	126	5911.6 (48.9)	97	6114.1 (16.8)	223
porcupine			1	15.0 (<1.0)	1
reedbuck	27	995.0 (8.2)	2	47.7 (<1.0)	29
steenbok	3	30.0 (<1.0)			3
striped polecat			2 [*]		2
suni			2	10.0 (<1.0)	2
warthog	6	171.0 (1.4)	104	5361.8 (14.7)	110
waterbuck			2	337.5 (<1.0)	2
wildebeest	10	903.6 (7.5)	110	12551.1 (34.6)	120
zebra	6	347.5 (2.9)	42	7279.0 (20.0)	48
Birds					
crested guinea fowl			1	1.2 (<1.0)	1
ostrich	1	72.0 (<1.0)	2	144 (<1.0)	3
wattled plover			1 [*]		1
Reptiles					
leopard tortoise			4 [*]		4
serrated hinged terrapin			2 [*]		2
TOTAL	325	12089.6kg	458	36287.1kg	783

Table 20: Complete list of all prey species of lions and cheetahs, Phinda, Winter 1992-Winter 1995. Data from observed kills and carcasses.

*Prey abandoned without eating, [‡]Partially eaten, [‡] 9 animals abandoned without eating, 3 fully eaten, 1 partially eaten, [†]1 animal eaten, others abandoned without eating, [§] 3 neonates eaten, 2 large cubs uneaten, [#] Exotic species.

**Edible biomass (kg), calculated by subtracting the estimated percentage of wastage (horns, large bones, stomach contents, etc.) from the average mass of each carcass. Percent wastage after Mills (1990), as follows: carcass weight >80kg = 33%, carcass weight 5-80kg = 10%, carcass weight 5kg = 0%. Figure in parenthesis shows percentage of total edible biomass. Carcass weight was estimated for every kill, according to age, sex and species using published data on herbivore weights (see Methods).

The four most important species for lions in terms of numbers killed were (in order) wildebeest, warthogs, nyalas and zebras (Table 20). It was the same four species in terms of biomass consumed, with wildebeest clearly the most important, followed by zebras, nyalas and warthogs. For cheetahs, nyalas, impalas and reedbucks were the most important species in terms of both numbers (82% of all kills) and biomass (81% of biomass).

Lions and cheetahs were observed on 783 kills, 525 (67%) of which they were known to have killed (Table 21). Cheetahs were never seen to scavenge and lions only scavenged on 8.8% of occasions where the origin of the carcass was certain. 17 scavenged carcasses were simply found by lions dead from unknown causes, four of them, warthogs which lions dug from burrows already dead. Three animals had died after being trapped in mud at the edge of pans. Four carcasses were appropriated from other carnivores (two from cheetahs, one from a leopard, one from a side-striped jackal) and four were killed by wire-snare and subsequently found by lions.

Carcass origin	Cheetah	Lion	Total
kill	235	290	525
scavenged	-	28	28
unknown	90	140	230
unobserved kills	156	112	268
TOTAL	481	570	1050

Table 21. Origin of carcasses on which lions and cheetahs fed. See Methods for explanation of terms.

I recorded 156 and 112 unobserved kills for cheetahs and lions respectively (Table 21). Most unobserved kills for cheetahs had estimated weights between 30-65kgs and for lions, it was greater than 120kgs (Table 22). As indicated in the methods, data on unobserved kills is heavily biased towards larger carcasses, particularly for lions.

Kill size	Weight range	Typical examples	Total
Cheetahs			
small	<30kgs	adult duikers & steenboks, juvenile nyalas and impalas.	18
medium	30-65kgs	juvenile zebras, wildebeest; sub-adult nyalas; sub-adult-adult impalas; adult female nyalas.	91
large	>65kgs	adult reedbucks & male nyalas; sub-adult wildebeest & zebras.	47
Lions			
small	<60kgs	impalas, warthogs, female nyalas; juvenile wildebeest & zebras.	8
medium	60-120 kgs	male nyalas, male warthogs; sub-adult wildebeest & zebras.	44
large	>120kgs	adult wildebeest, kudu; sub-adult/adult zebras, giraffes.	60

Table 22. Details of unobserved kills for lions and cheetahs.

	giraffe	impala	kudu	nyala	reedb'k	w'thog	wildeb	zebra	Chi-square
Relative abundance	1.1%	29.5%	4.0%	33.2%	1.2%	13.3%	9.8%	8.0%	
Lion kills	8 (2.1%)	20 (5.4%)	14 (3.8%)	97 (23.6%)	2 (0.6%)	104 (27.5%)	110 (28.2%)	42 (8.9%)	$\chi^2 = 31.014,$ $p < 0.000, df = 7$
Predation rating ^a	1.9	0.2	0.9	0.7	0.5	2.1	2.9	1.1	
Cheetah kills	2 (0.7%)	122 (38.3%)	5 (1.7%)	126 (42.4%)	27 (9.3%)	6 (2.1%)	10 (3.4%)	6 (2.1%)	$\chi^2 = 39.227,$ $p < 0.000, df = 7$
Predation rating ^a	0.6	1.3	0.4	1.3	7.75	0.2	0.3	0.3	

Table 23. Population and kill ratios of eight common prey species of lions and cheetahs. Relative abundance figure is calculated from population estimates only of these eight species at Phinda.

^a kill frequency divided by relative abundance (after Pienaar, 1969 who termed it 'preference rating.' See Discussion for details).

Both lions and cheetahs did not prey on eight common species of herbivores at the frequency with which they occurred in Phinda (Table 23). Lion predation was greater on wildebeest and warthogs, and less on impalas and reedbucks than expected from their availability. Predation on giraffes, kudus, nyalas and zebras reflected their availability. Cheetahs preyed upon the two most important species (in terms of number of kills and biomass), nyalas and impalas, at approximately their relative availability. Reedbucks (cheetahs' third most important prey species) were preyed upon at almost eight times their availability. Predation was less than expected from availability for all other species.

Patterns of Lion Predation.

Lions preyed on male and female ungulates at the frequency they occurred in Phinda in impalas, wildebeest and zebras (Table 24). This did not apply for three other ungulate species: lions killed male kudus, male nyalas and male warthogs at significantly greater frequencies than their availability would predict. For most ungulates, lions preyed on age classes as they occurred (Table 25): however, predation on giraffes, nyalas and zebras was generally heavier on juvenile or subadult age classes.

Prey species	Kills		Population		Chi-square
	Female	Male	Female	Male	
Common ungulates*					
giraffe	3 (100%)	0 (0%)	59.3%	40.7%	-
impala	10 (62.5%)	6 (37.5%)	72.8%	27.2%	$\chi^2 = 0.802, p = 0.370, df = 1$
kudu	2 (16.6%)	10 (83.3%)	68.6%	31.2%	$\chi^2 = 15.508, p < 0.000, df = 1$
nyala	27 (28.7%)	67 (71.3%)	64.5%	35.5%	$\chi^2 = 52.430, p < 0.000, df = 1$
reedbuck	1 (100%)	0 (0%)	73.3%	26.7%	-
warthog	36 (48.6%)	38 (51.4%)	60.6%	39.4%	$\chi^2 = 4.380, p = 0.036, df = 1$
wildebeest	67 (75.3%)	22 (24.7%)	71.4%	22.6%	$\chi^2 = 0.673, p = 0.411, df = 1$
zebra	12 (80.0%)	3 (20.0%)	77.4%	22.6%	$\chi^2 = 4.734, p = 0.295, df = 1$
Other					
bushpig	7	2			-
grey duiker	2	1			-
ostrich		2			-
porcupine					-
red duiker	2	2			-
sunni		2			-
waterbuck	1	1			-

Table 24. Lion prey by sex classes. *'Common ungulates' refers to the eight species which I censused regularly and hence for which I have population data suitable for analysis (see Chapter 7 for details). Chi-squared result shows comparison between incidence in kills by lions on different sexes and frequency of occurrence in the population. Significant differences at $p \leq 0.05$ are shown in bold-type. Dashes indicate too few data for analysis.

Prey species	Kills			Population			Chi-square
	Juvenile	Sub-adult	Adult	Juvenile	Sub-adult	Adult	
Common Ungulates							
giraffe	5 (62.5%)	1 (12.5%)	2 (25.0%)	7.7%	8.6%	83.7%	-
impala	3 (15.0%)	6 (30.0%)	11 (55.0%)	11.4%	16.6%	71.9%	$\chi^2 = 3.224$, p= 0.199, df= 2
kudu	2 (14.3%)	0 (0%)	12 (85.7%)	11.7%	8.9%	79.4%	$\chi^2 = 1.372$, p= 0.503, df= 2
nyala	2 (2.1%)	14 (14.4%)	81 (83.5%)	13.5%	9.8%	76.7%	$\chi^2 = 12.122$, p= 0.002, df= 2
reedbuck	1 (50.0%)	0 (0%)	1 (50.0%)	6.7%	5.5%	87.8%	-
warthog	15 (14.4%)	14 (13.5%)	75 (72.1%)	16.9%	16.7%	66.4%	$\chi^2 = 1.570$, p= 0.456, df= 2
wildebeest	18 (16.4%)	19 (17.3%)	73 (66.3%)	11.5%	14.9%	73.6%	$\chi^2 = 3.376$, p= 0.184, df= 2
zebra	9 (21.4%)	1 (2.4%)	32 (76.2%)	10.2%	9.7%	80.1%	$\chi^2 = 7.135$, p= 0.028, df= 2
Other							
bushpig	1	6	6				-
grey duiker	1		3				-
ostrich			2				-
porcupine			1				-
red duiker			6				-
suni			2				-
waterbuck			2				-

Table 25. Lion prey by age-classes compared to frequencies in the population. Juveniles were animals born in the previous natal season for seasonal breeders or animals less than a year of age for aseasonal breeders. Sub-adults were animals estimated to be older than a year and less than 3 or 4 years depending on the species. Other details as for legend, Table 24.

Prey species	DMB	Grass	MBC	MBO	Palm	RSC	RSO	RF	SF	Chi-squared result
giraffe	2		2	2					1	-
impala	1 (0.63)	5 (4.5)	3 (1.45)	5 (4.26)	1 (2.4)	3 (1.82)	1 (2.98)	0 (0.53)	0 (0.44)	$\chi^2 = 5.93, p = 0.362, df = 8$
kudu	1 (1.41)	1 (1.09)	5 (4.98)	1 (2.48)	2 (0.92)	2 (1.55)	2 (1.54)	0 (0)	0 (0)	$\chi^2 = 2.54, p = 0.959, df = 8$
nyala	0 (0.94)	10 (5.78)	12 (12.84)	9 (14.96)	3 (1.7)	27 (20.49)	14 (18.87)	5 (0.94)	5 (10.12)	$\chi^2 = 30.896, p < 0.000, df = 8$
reedbuck					1	1				-
warthog	5 (0)	17 (19.1)	28 (22.2)	27 (29.4)	11 (10.7)	3 (8.8)	6 (9.9)	1 (0)	2 (0)	$\chi^2 = 7.309, p = 0.504, df = 8$
wildebeest	6 (6.34)	26 (26.62)	13 (15.70)	26 (27.14)	10 (12.17)	3 (4.99)	15 (10.4)	4 (0.73)	1 (0)	$\chi^2 = 18.408, p = 0.018, df = 8$
zebra	5 (1.08)	9 (10.84)	8 (4.44)	6 (8.88)	5 (5.24)	3 (3.08)	1 (4.44)	1 (1.11)	2 (0.88)	$\chi^2 = 22.444, p = 0.004, df = 8$
other	1	7	8	11	11	11	3	1		-
TOTAL	21 (5.0%)	75 (17.7%)	79 (18.6%)	87 (20.5%)	44 (10.4%)	53 (12.5%)	42 (9.9%)	12 (2.8%)	11 (2.6%)	

Table 26. Lion kills made in each habitat type. Figure in parenthesis is expected number of kills in each habitat type, calculated from estimated ungulate densities per habitat type (from seasonal censuses; Chapter 7). Chi-squared figure is the result of comparing observed to expected kills in each habitat. Significant results at $p < 0.05$ are shown in boldtype. Dashes indicate inadequate data for analysis.

Excluded are scavenged carcasses and six animals driven into artificial pools.

Habitat types are described in Chapter 2: DMB = dry mountain bushveld; Grass = grasslands; MBC = closed mixed bushveld; MBO = open mixed bushveld; Palm = palmveld; RSC = closed red sand bushveld; RSO = open red sand bushveld; RF = riparian forest; SF = sandforest.

Lions made most of their kills in grasslands and open or closed mixed bushveld. Lions killed nyalas, wildebeest and zebras at different frequencies to that predicted by their occurrence in different habitats. Nyalas were killed in grasslands and riparian forests at greater than expected frequencies, and in open mixed bushveld and sandforest at lower than expected frequencies. Wildebeest were killed in greater than expected frequencies in riparian forest and open red sand bushveld. Zebras were killed in dry mountain bushveld and closed mixed bushveld at greater than expected frequencies, and in open red sand bushveld at lower frequencies than expected.

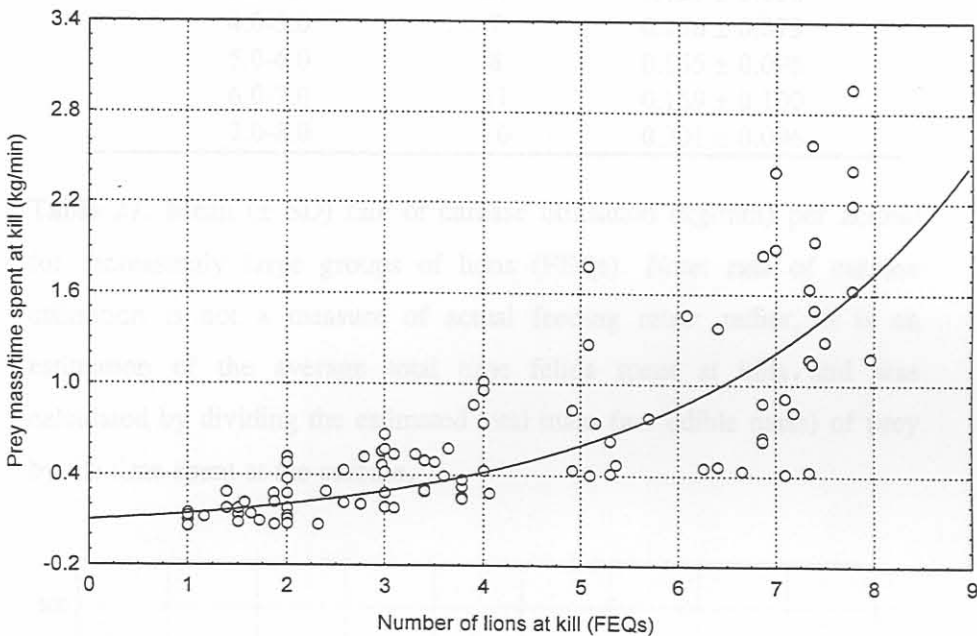


Figure 38. Scatter diagram showing relationship between time spent on kills of different weights and number of lions feeding (expressed as FEQs). Fitted function: $y = 0.101\exp(0.355x)$, $r^2 = 0.5805$.

There was a curvilinear relationship between the number of lions on a kill and carcass utilisation, increasing for larger groups (Fig 38). Although there was no statistically significant difference between the amount of time spent per individual on kills of different masses for increasing FEQs (Kruskal-Wallis $H = 11.353$, $p = 0.078$, $df = 6$, $n = 98$), there was a clear trend showing this time decreased: the rate of carcass utilisation almost doubled from groups numbering 1-2 to groups of 7-8, probably reflecting faster rates of consumption due to increased competition at kills (Table 27).

Accordingly, although it was not statistically significant, the likelihood of opportunistically locating lions on small kills decreased with increasing FEQs. However, given that small kills generally make an insignificant contribution to lions' total food intake (Packer *et al*, 1990; Scheel, 1993; Scheel & Packer, 1994) and that the relationship between the number of lions on a kill and the mass of the kill was unlikely to be significant even with a greater sample of small kills, (see below), I have proceeded with this analysis (lion numbers vs prey mass) and discuss its limitations below.

Number of lions on kill	<i>n</i>	Rate of carcass utilisation
1.0-2.0	18	0.111 ± 0.041
2.0-3.0	17	0.124 ± 0.072
3.0-4.0	21	0.123 ± 0.050
4.0-5.0	7	0.156 ± 0.073
5.0-6.0	8	0.155 ± 0.096
6.0-7.0	11	0.169 ± 0.100
7.0-8.0	16	0.201 ± 0.096

Table 27. Mean (± SD) rate of carcass utilisation (kg/min) per animal for increasingly large groups of lions (FEQs). *Note:* rate of carcass utilisation is not a measure of actual feeding rates: rather, it is an estimation of the average total time felids spent at kills and was calculated by dividing the estimated total mass (*not* edible mass) of prey by the time spent at the carcass.

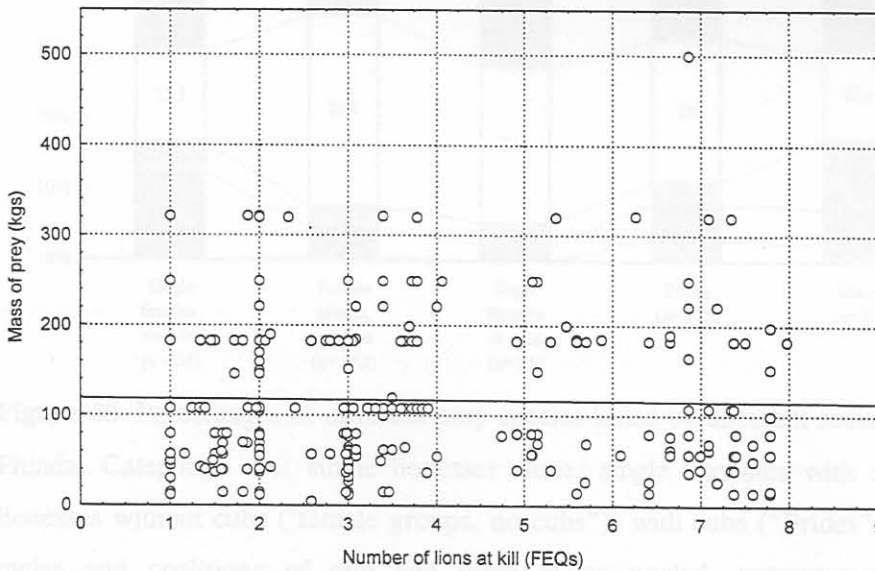


Figure 39. Scatter diagram showing relationship between number of lions feeding on kills (expressed as FEQs) and the prey mass. $F = 0.0421$, $p = 0.8374$, $df = 1$, $r^2 > 0.00$. $n = 321$.

Lions did not show any relationship between the mass of prey species killed and number of lions at the kill when expressed as FEQs (Fig. 39). However some differences emerged when comparing females alone or with cubs (Fig. 40). 20.8% of lone females' kills were of 'other' prey species (i.e. species other than the eight common large ungulates at Phinda). These species were largely small ungulates, particularly grey and red duiker, which only constituted 6.6% of kills made by single females when they had cubs and 6.7% of kills by prides (though the greater chance of finding small kills by single females compared to groups must be noted). 86.6% of kills by single females with cubs were of wildebeest, warthog and nyala: for lone females this was 54.1%. For prides, warthog, wildebeest and nyala constituted 73.3% of all kills and the percentage of zebras and giraffes killed increased. Males unaccompanied by females killed more large species (particularly zebras and kudus) and fewer warthogs and nyalas than female groups.

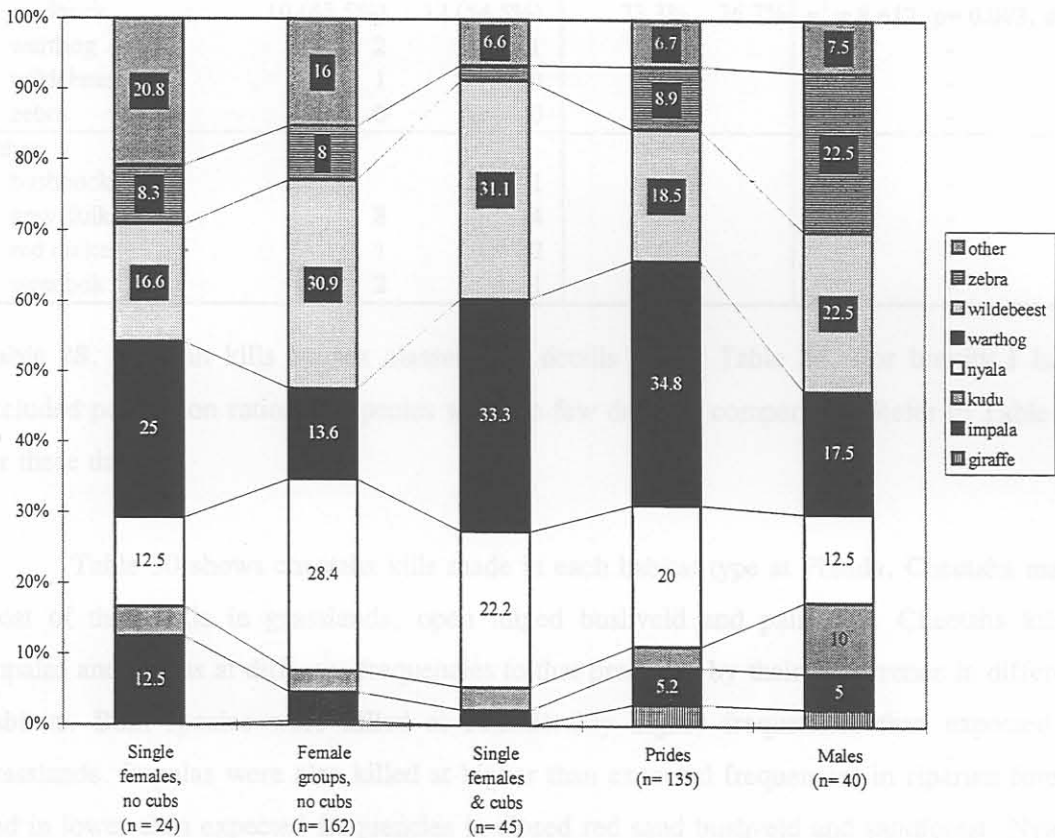


Figure 40. Percentages of different prey species killed by different social groups of lions at Phinda. Categories are: single lionesses alone, single lionesses with cubs, two or more lionesses without cubs ("female groups, no cubs"), with cubs ("Prides") and males (single males and coalitions of two and three males pooled, unaccompanied by females). Reedbucks are included in 'other' prey category as only two kills of this species were recorded, both by female groups with no cubs. *n* is number of kills for each category.

Patterns of cheetah predation

I analysed predation by cheetahs on sex-age cohorts only for three species (impalas, nyalas and reedbucks) as kills of the other common species were too infrequent to allow this analysis. Cheetahs preyed on male and female ungulates at the frequency they occurred in Phinda except for reedbuck in which predation on males was greater than expected (Table 28). Predation in all three species was greater on juvenile age classes than expected from availability (Table 29).

Prey species	Kills		Population		Chi-square
	Female	Male	Female	Male	
Common ungulates					
giraffe	?	?			-
impala	47(67.1%)	23(32.9%)	72.8%	27.2%	$\chi^2 = 4.813, p = 0.282, df = 1$
kudu	1	0			-
nyala	51 (56.0%)	40 (44.0%)	64.5%	35.5%	$\chi^2 = 3.428, p = 0.064, df = 1$
reedbuck	10 (45.5%)	12 (54.5%)	73.3%	26.7%	$\chi^2 = 8.617, p = 0.003, df = 1$
warthog	2	1			-
wildebeest	1	0			-
zebra	0	0			-
Other					
bushbuck		1			-
grey duiker	8	4			-
red duiker	1	2			-
steenbok	2	1			-

Table 28. Cheetah kills by sex classes. All details as for Table 24. For brevity I have excluded population ratios for species with too few data for comparison. Refer to Table 24 for these data.

Table 30 shows cheetahs kills made in each habitat type at Phinda. Cheetahs made most of their kills in grasslands, open mixed bushveld and palmveld. Cheetahs killed impalas and nyalas at different frequencies to that predicted by their occurrence in different habitats. Both species were killed at considerably higher frequencies than expected in grasslands. Impalas were also killed at higher than expected frequencies in riparian forests and in lower than expected frequencies in closed red sand bushveld and sandforest. Nyalas were also killed by cheetahs in higher frequencies than expected in palmveld and dry mountain bushveld, and in lower than expected frequencies in closed red sand bushveld and sandforest.

Prey species	Kills			Population			Chi-square
	Juvenile	Sub-adult	Adult	Juvenile	Sub-adult	Adult	
Common ungulates							
giraffe	2	0	0				-
impala	41 (36.6%)	18 (16.1%)	53 (47.3%)	11.4%	16.6%	71.9%	$\chi^2 = 71.598, p < 0.000, df= 2$
kudu	4	0	1				-
nyala	35 (27.9%)	21 (16.6%)	70 (55.5%)	13.5%	9.8%	76.7%	$\chi^2 = 32.537, p < 0.000, df= 2$
reedbuck	5 (18.5%)	4 (14.8%)	18 (66.6%)	6.7%	5.5%	87.8%	$\chi^2 = 7.357, p = 0.025, df= 2$
warthog	2	4	0				-
wildebeest	8	2	0				-
zebra	5	1	0				-
Other							
bushbuck	0	1	0				-
grey duiker	2	0	13				-
red duiker	1	0	7				-
steenbok	0	0	3				-

Table 29. Cheetah kills by age classes. All details as for Table 25.

Prey species	DMB	Grass	MBC	MBO	Palm	RSC	RSO	RF	SF	Chi-squared result
giraffe	1				1					-
impala	1 (3.70)	37 (26.54)	10 (8.51)	27 (25.09)	10 (14.11)	6 (10.75)	14 (17.58)	7 (3.14)	(2.53)	$\chi^2 = 17.790$, $p = 0.022$, $df = 8$
kudu			3	1		1				-
nyala	4 (1.39)	25 (8.57)	14 (19.02)	26 (22.17)	18 (2.52)	10 (30.36)	22 (27.97)	2 (1.39)	5 (14.99)	$\chi^2 = 155.33$, $p < 0.000$, $df = 8$
reedbuck	(0)	16 (14.77)	1 (0.59)	3 (1.38)	5 (7.85)	1 (0)	(0.92)	(1.48)	1 (0)	$\chi^2 = 5.724$, $p = 0.678$, $df = 8$
warthog	1	2	1		2					-
wildebeest		7		2	1					-
zebra		4	2							-
other	1	7	3	7	5		4		2	-
TOTAL	8 (2.5%)	98 (30.3%)	34 (10.5%)	66 (20.4%)	42 (13.0%)	18 (5.6%)	40 (12.4%)	9 (2.8%)	8 (2.5%)	

Table 30. Cheetah kills made in each habitat type. Excluded are two cheetahs. All other details as for legend, Table 6.7

There was a strong relationship between the time spent on kills of different mass by cheetah females with cubs (Fig. 41). Not surprisingly, the time spent on kills decreased relatively linearly with increasing group size. There was no significant difference between the amount of time spent per individual on kills of different masses for increasing FEQs (Kruskal-Wallis $H = 7.87$, $p = 0.248$, $df = 6$, $n = 100$), suggesting that the likelihood of locating cheetahs with kills of different masses was approximately equal for increasing FEQs (Table 31). In other words, although opportunistic location of cheetah kills was biased towards finding larger kills, the relative likelihood of finding small kills did not significantly decrease with increasing group size.

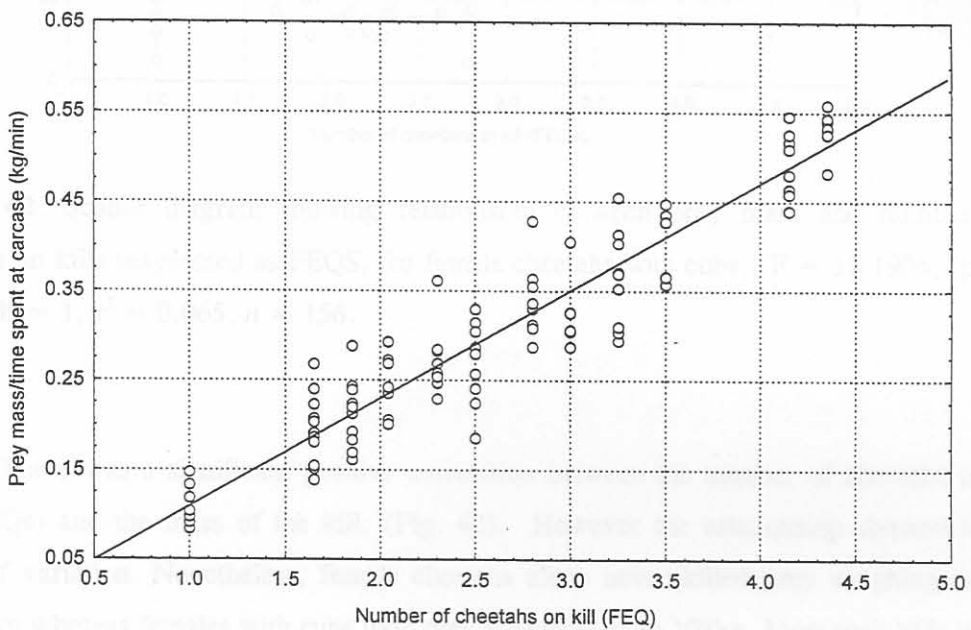


Figure 41. Scatter diagram showing relationship between time spent on kills of different weights and number of cheetahs feeding (expressed as FEQs) for cheetah females with cubs. Fitted function: $y = 0.011 + 0.012x$, $r^2 = 0.899$, $n = 100$.

Number of cheetahs on kill	<i>n</i>	Rate of carcass utilisation
<1.5	10	0.106 ± 0.019
1.5-2.0	21	0.117 ± 0.022
2.0-2.5	17	0.120 ± 0.016
2.5-3.0	17	0.114 ± 0.018
3.0-3.5	15	0.110 ± 0.015
3.5-4.0	5	0.116 ± 0.012
4.0-4.5	15	0.120 ± 0.007

Table 31. Mean (± SD) rate of carcass utilisation (kg/min) per individual for increasingly large groups of cheetah females and cubs (FEQs). All other details as for Table 27.

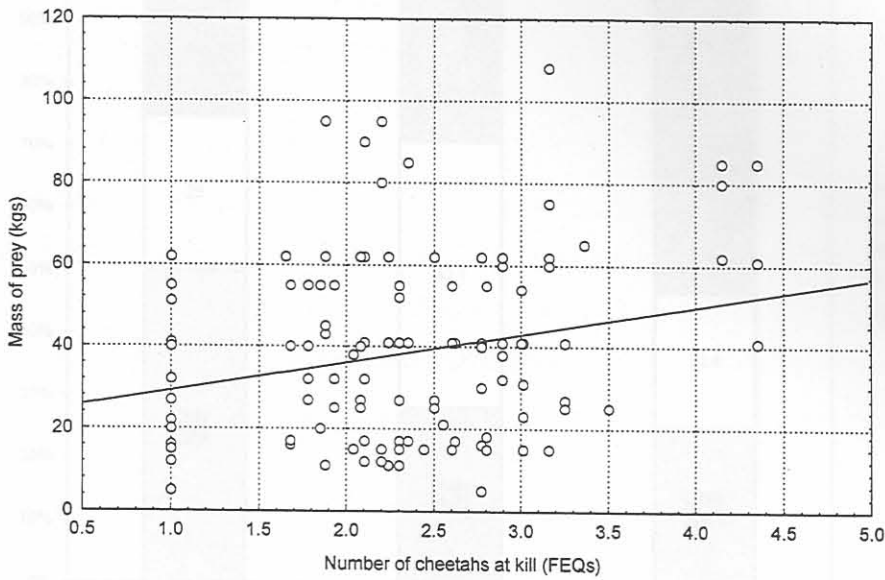


Figure 42. Scatter diagram showing relationship between prey mass and number of cheetahs on kills (expressed as FEQs) for female cheetahs with cubs. $F = 11.1906$, $p > 0.001$, $df = 1$, $r^2 = 0.065$, $n = 156$.

There was a significant positive correlation between the number of cheetahs on a kill (FEQs) and the mass of the kill. (Fig. 42). However the relationship showed high levels of variation. Nonetheless, female cheetahs alone never killed prey weighing more than 62kg whereas females with cubs took prey weighing up to 108kg. Most such kills were male reedbucks or male nyalas which were only killed by females when they had cubs. Prey weighing less than 20kg constituted 50.0% of kills made by lone females whereas for mothers, this figure was 28.2% (Fig. 43.). Females only made one kill weighing more than 100kgs, an adult bull nyala killed by a female with four 10mo cubs (FEQ = 3.16). In contrast, kills weighing more than 100kg constituted 23.4% of catches made by coalitions of male cheetahs and ranged up to adult female wildebeest with an estimated weight of 185kgs (Fig. 43)

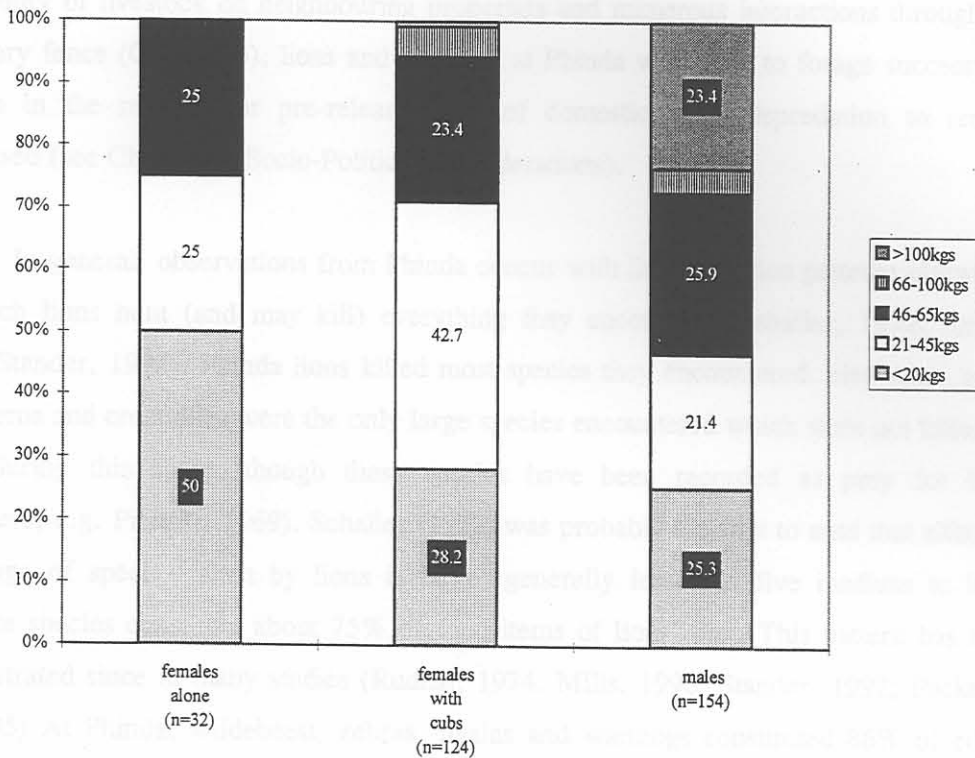


Figure 43. Percentage of cheetah kills of different mass for lone females, females with cubs and males. n is number of kills. All data for males are from coalitions (pairs and trios).

DISCUSSION.

The availability of food resources is one of the primary requirements for successful reintroduction of any species (Kleiman, 1989; Reading & Clark, 1996). This is particularly pertinent for large carnivores where the frequency with which translocated or reintroduced carnivores predate stock is a factor for considerable concern (Ruth *et al*, 1993, Reading & Clark, 1996; Linnell *et al*, 1997). Although other factors such as a lack of available social space and a history of stock-predation are contributory factors in many cases, increased conflict with humans is likely to occur during shortages of available natural food. Chivers (1991) has noted the importance of food resources being available year-round and consistently enough in the first few years to encourage re-population and reduce the potential for clashes with people. Reintroduced lions and cheetahs at Phinda clearly had no difficulty in foraging following their release. Suitable prey species and abundance existed at Phinda for post-release survival of lions and cheetahs (see Chapter 5) to be free of constraints related to food resources or their feeding ecology. Additionally, despite the

availability of livestock on neighbouring properties and numerous interactions through the boundary fence (Chapter 3), lions and cheetahs at Phinda were able to forage successfully enough in the reserve for pre-release fears of domestic stock depredation to remain unrealised (see Chapter 2: Socio-Political Considerations).

In general, observations from Phinda concur with lion predation patterns elsewhere in which lions hunt (and may kill) everything they encounter, (Schaller, 1972; Smuts, 1982; Stander, 1992). Phinda lions killed most species they encountered: elephants, white rhinoceros and crocodiles were the only large species encountered which were not killed by lions during this study (though these species have been recorded as prey for lions elsewhere, e.g. Pienaar, 1969). Schaller (1972) was probably the first to note that although the range of species taken by lions is large, generally less than five medium to large ungulate species constitute about 75% of food items of lions' diet. This pattern has been demonstrated since in many studies (Rudnai, 1974; Mills, 1990; Stander, 1992; Packer *et al.*, 1995) At Phinda, wildebeest, zebras, nyalas and warthogs constituted 86% of edible biomass consumed by lions and made up 77% of all carcasses. Of those species, lions killed wildebeest and warthogs at greater frequencies than occurrence and zebras and nyalas at approximately their occurrence.

Prey preference for lions (Pienaar, 1969; Rodgers, 1974; Rudnai, 1974; Berry, 1981) has been presented as a Preference Rating (PR) calculated where $PR = \text{kill frequency} / \text{relative abundance of prey}$ (Table 23). Stander (1992) suggested this is rather an indication of prey vulnerability to a predator and is subject to factors such as the spatial distribution of prey and hunting success on different prey species (Sunquist & Sunquist 1989; Stander, 1992). Actual preferences for a prey species or type are difficult to demonstrate unless direct observation permits an assessment of an actual selection being made by predators when faced with a choice of prey species. This was rarely possible during the current study due to dense vegetation where it was difficult to follow hunting lions and where it was frequently impossible to determine which prey species were present when lions actually began their stalk. I saw 14 occasions where lions apparently made direct movements of 1-2km from areas of dense vegetation (where small cubs were hidden), to open areas with high wildebeest and zebra densities. In all cases, lions encountered smaller prey species (usually impalas and nyalas) at distances of <100m on their way, but made no hunting attempt and proceeded to the wildebeest/zebra herds. While this suggests lions were actively searching for large species and ignoring smaller ones, there may be many factors contributing to such a pattern and I do not have the sample size to examine the question in detail.

However, the importance of wildebeest to lions at Phinda was evident. Wildebeest were preyed upon at three times their relative abundance and made up more than one-third of the edible biomass killed by lions. As a result of lion predation, wildebeest underwent a considerable population decline during the study period (Chapter 7). Given the small group size of lions at Phinda, the low risk of losing kills to competitors and the far greater abundance of other prey species particularly nyalas and impalas, it is interesting that lions still appeared to 'prefer' larger prey. Lions at Phinda showed no relationship between pride size and prey mass (Fig. 39): different sized groups killed all prey sizes at essentially the same frequency with an emphasis towards larger species. Although single lionesses killed more very small species, this may have been a sampling artefact in that I was more likely to find small kills made by lone lionesses. In Etosha National Park in Namibia, Stander (1992) showed that lions hunting in pairs could meet their minimum daily requirements (5-8.5kg per day: Packer *et al* 1990) by hunting mostly springboks weighing <50kg. Presumably, the small groups at Phinda *could* have foraged efficiently by merely taking the most abundant ungulate, the nyala, or even impalas (the second most abundant species) both of which are heavier than springboks. Importantly, habitat use by nyalas differed markedly to that by wildebeest (Chapter 7) and lions generally preferred habitats used by wildebeest (Chapter 4) and made proportionately more kills there than in habitats where nyala density was highest (Table 26). Accordingly wildebeest may have been 'preferred' by lions simply because they were encountered by lions at greater rates than nyalas. However, two points suggest this is unlikely. Nyalas outnumbered wildebeest at Phinda by a factor of 3.4 and their density in each habitat far exceeded wildebeests' in all habitats except dry mountain bushveld and grassland (in which density of each species was close to parity) and palmveld in which density of wildebeest was greater (Chapter 7). Secondly, impala habitat use is generally very similar to wildebeests' (Hirst, 1975) which was the case for this study (Chapter 7) and their far greater density in all habitats suggests lions should have been more likely to kill them than wildebeests if encounter rate alone was the critical factor.

Smuts (1982) characterised lion predation patterns as favouring the 'easiest' prey and perhaps wildebeest were simply easier for lions to catch. Wildebeest looked less often than impalas and spent less time on average per scan than impalas (Chapter 8), so they were possibly easier for lions to approach undetected. Furthermore, single lionesses alone are able to subdue all prey species that groups of lions take except for the very largest quarry (Packer *et al*, 1990; Stander, 1992) and only adult buffaloes, giraffes and occasionally zebras present a danger to lions. Lions were never observed to incur injuries during hunts of wildebeests, and wildebeest never escaped once caught by a lion as zebras may do (Rudnai, 1974; Berry, 1980; present study). This suggests that while hunting

wildebeest, they probably expended little extra energy and presented little increased risk than when hunting nyalas, and therefore hunting wildebeest maximised the amount of food received per hunt. However, it would require specific data such as the success rates of hunting different species, the time spent and the frequency hunting different species and the risk of injury hunting different species to confirm this, data which I do not have for this study. Assuming the risk and effort is similar for the two prey species, wildebeest would clearly be a far more valuable resource for lions. Lions rarely abandon kills before they are entirely consumed and only lost two kills to hyaenas during this study. Therefore, a pair or trio of lions could remain at a wildebeest kill for 3-4 days and then not need to hunt for some days following. Although lions could almost certainly have foraged efficiently at Phinda if they had hunted mostly smaller prey, the patterns observed here confirm Stander's (1992) suggestion that even when smaller prey is available, lions show a preference for large prey when opportunity permits.

This may have important management implications for reserves introducing predators or wishing to manage predator-prey interactions and populations. Van Dyk (1997) has suggested that manipulating sizes of prides in reintroduced populations can be a valuable technique for reducing predation on large (and generally valuable) prey species. Although this applies for very large prey species such as giraffes and buffaloes which require large pride sizes to hunt successfully (Packer *et al*, 1990), managers should not necessarily assume that an abundance of smaller prey species will reduce predation on species such as wildebeest or similarly-sized rarer species, for example, roan and sable. Van Ordsol showed that lions in two regions of Queen Elizabeth National Park, Uganda opportunistically hunted small prey (particularly warthogs) during the day but at night actively searched for large prey, in doing so maximising the amount of food received per kill. At Phinda, it appears lions hunted small-medium sized prey, particularly warthogs and nyalas opportunistically, but invested greater effort in searching for larger species.

Not surprisingly, cheetahs at Phinda were far more selective than lions in terms of species. Excluding two male cheetahs killed in intra-specific fights, all species killed by cheetahs (except for one male ostrich) and more than 99% of all kills were ungulates. 81% of kills in terms of biomass (and 82% of all kills in numbers) comprised three species: nyalas, impalas and reedbucks. Despite extensive overlap in ranges and regular encounters (Chapter 4), cheetahs at Phinda rarely came into direct competition with lions for food resources, which may have contributed to cheetahs' success during this study. Cheetahs lost only two kills to lions and abandoned a kill on one other occasion when lions passed nearby

but did not see the cheetahs. Incidentally, cheetahs lost kills to other predators on two occasions, once each to a leopard and a spotted hyaena.

Durant (1998) recently demonstrated the importance of local avoidance behaviour by cheetahs in both space and time with respect to lions and hyaenas. The most abundant ungulate at Phinda, nyalas, featured prominently in both lions' and cheetahs' diet, and therefore the potential for competition was considerable. Nyalas are always found in association with dense thickets and at Phinda, were at their greatest densities in *Acacia* woodlands and Red sand bushveld (Chapter 7) which is where lions mostly killed them (Table 26). However they also commonly graze in more open habitats, although never more than a few hundred metres from cover (Tello & Van Gelder, 1975), suggesting they are vulnerable to predation in the open. Cheetahs probably reduced competition with lions for nyalas by hunting them largely in open habitat such as grassland and palm veld (Table 30). Although cheetahs were able to hunt in much denser vegetation, nyalas are sluggish runners compared to many other antelopes and seemed easily captured when cheetahs pursued them in the open. On the other hand, lions made relatively few nyala kills in the open and nyalas often out-ran them in grasslands and palm veld.

The lack of direct competition experienced by cheetahs was manifested in other ways. Cheetahs rarely abandoned kills before they were satiated, commonly spending 12-14 hours on large carcasses. On one occasion, two males ate from a juvenile giraffe kill for 28 hours. Furthermore, cheetahs sometimes returned to large kills after abandoning them overnight (presumably to avoid nocturnal predators such as lions and hyaenas), resting up to 500m away and returning to them the following morning. This has been rarely reported where the density of competitors is high and cheetahs suffer from high rates of kleptoparasitism (Graham, 1965; Burney, 1980). I saw 12 incidents when this occurred, all of them by females when accompanied by large litters of adult-sized cubs. Laurenson (1992) demonstrated that females with cubs younger than 2 months hunted more 'large prey' (>20kgs) and were more successful during hunts of large prey than lone females. Mother's preferences for large prey such as adult Thomson's and Grant's gazelles persisted until the cubs were 8.5 months old and then declined, probably because the most expensive energetic stage for mothers was during lactation (Caro, 1994). I do not have data this specific but there was a positive relationship between litter size/age (as measured by FEQs) and prey mass, (although there was very high variation around the relationship, see Figure 42). Lone females never killed prey greater than 62kgs (the mean weight of adult female nyalas) and all kills weighing more than 75kgs (except for one) were made by females with cubs whose combined FEQ was equivalent to at least another adult female. At Phinda, the high survival rate of cubs meant that females probably experienced increased energetic

demands as cubs approached adult size or else energetic demands remained high after lactation had ceased. Unlike most Serengeti mothers where juvenile mortality may be as high as 95% (Laurenson 1992), Phinda females with many large cubs had to provide for the equivalent of up to 3-4 other adult females (in terms of mass). Large cubs rarely contributed to hunts or even to subduing prey once it was caught. Although females caught small prey which they brought alive to the cubs to 'practise on' from when the cubs were 6 months old, I never saw females relinquish large kills to cubs until the animal had been suffocated. Therefore, mothers appeared to bear the substantial energetic demands of killing large animals on their own. At Phinda, mother cheetahs appeared to offset this cost by hunting very large prey, eating from it until it was finished and, in some cases, returning to the carcass when there was still meat on it.

These behaviours probably had considerable costs. I saw female cheetahs injured in successful hunts on 17 occasions: 15 of them were during hunts on prey larger than 60kgs. Although it was rarely possible to determine how cheetahs received injuries, twice I saw females tumble bodily with large prey (both adult male reedbucks) once they had caught it and incur injuries on both occasions. However, I cannot say whether other factors such as the density of vegetation or the continuity of the terrain contributed to the likelihood of injury. Incidentally, all cheetahs which I saw injured during hunts always recovered. Presumably, the risks of hunting large prey were outweighed by the benefits of acquiring a large carcass which, in the absence of competition, could be utilised fully. Interestingly, I never observed cheetahs to scavenge carcasses which is generally very rare behaviour (Pienaar, 1969; Caro, 1982) but which, presumably, they may have done safely at Phinda given the lack of competing predators. I only observed one occasion when cheetahs encountered an animal which had died of natural causes (impala female). It was starting to putrefy and the cheetahs left it after a very cautious approach and exploratory sniff. Interestingly, cheetahs always took fresh carcasses offered to them when I needed to dart them.

Patterns of predation by male cheetahs suggested similar aspects of 'predator release.' Almost one-quarter of kills made by male coalitions weighed more than 100kgs and I only noted eight occasions when males left kills before they were finished, 50% of which were due to males being chased from kills by other carnivores. Most of the large kills made by males were nyalas and the presence of this species at Phinda contributed significantly to patterns of cheetah predation observed here. Caro (1994) has demonstrated that large gaps in the size distribution of abundant prey determine patterns of prey selection and hunting rates in Serengeti cheetahs. Such gaps "help to explain why individual foraging returns rise with group size in (smaller) male cheetahs but decline or remain static in

(larger) lionesses” (Caro, 1994:274). In the Serengeti, single males could meet their foraging needs by preying on Thomson’s gazelles, pairs needed to switch to young wildebeests and trios had to kill nothing smaller than a yearling wildebeest to satisfy their needs. However, wildebeests are a dangerous species for cheetahs to hunt. Caro mentions five occasions where cheetahs were kicked, butted or tossed by wildebeest (Caro 1994:276). I saw yearling/sub-adult wildebeest turn to face cheetahs on six occasions after the cheetahs had actually caught them and the wildebeest escaped. On two occasions, I saw adult wildebeest attempt to drive cheetahs from their catch of juvenile wildebeest, vigorously trying to butt or horn cheetahs (but failing). I also saw three occasions when wildebeest herds chased single cheetahs walking nearby.

At Phinda, the most abundant ungulate species was nyala (Chapter 7) which weighs 120-130kgs in the males and 60-70 kgs in the females, yet nyalas did not appear to present the risks entailed in hunting wildebeest. Despite their impressive horns, nyalas seem easily subdued and very rarely made any effort to defend themselves. I only saw one occasion when a male nyala defended itself from attack by cheetahs, three siblings recently separated from their mother. The nyala backed into an *Acacia nylotica* thicket and rushed the cheetahs with horns lowered whenever the cheetahs approached. The cheetahs eventually gave up, though an adult coalition may have been able to subdue the nyala (which, incidentally, was totally blind). Despite the ease with which cheetahs appeared to prey on nyalas at Phinda, male nyalas were too large or too dangerous for female cheetahs. Male cheetahs in coalitions killed mostly male nyalas (58.6% of adult or sub-adult nyalas killed) whereas female cheetahs killed mostly female nyalas (79.9% of adult or sub-adult nyalas killed).

As an abundant, large prey species easily caught with relatively little risks, the nyala represented a highly profitable resource for cheetahs. Nyalas constituted almost 50% of kills made by cheetahs (in terms of biomass) which was more than double the next most important prey species, impalas (23.8%; Table 20), often the most important prey species in other systems (eastern Transvaal, South Africa: Hirst, 1969; Pienaar, 1969, Nairobi National Park, Kenya: McLaughlin, 1970; Eaton, 1974). This is the first study of cheetah feeding ecology to illustrate that cheetahs can specialise on a relatively large, heavy ungulate. Although cheetahs from other studies are well-known to take prey as large as the largest taken at Phinda, in all other comprehensive studies of their feeding ecology, the most important prey species generally weighed less than 60kgs in the male (e.g. impalas) and was often as small as 20kg (e.g. Thomson’s gazelle). Although cheetahs are the most specialised felid, preferring small to medium sized gazelle-type prey, particularly in open grassland where most studies have been undertaken (Caro, 1994; Nowell & Jackson,

1996), the patterns observed at Phinda illustrate they are flexible and efficient hunters in woodland-dominated habitat and are not necessarily dependent on gazelle or impala-sized prey to be successful. Comparisons with cheetah populations in other woodland habitats would be especially interesting, particularly where the prey base differs to that at Phinda and where attempts are ongoing to re-establish cheetahs (such as at Pilanesberg National Park and Madikwe Game Reserve).

Some male ungulates at Phinda were more vulnerable than females to predation by both cheetahs and lions. Lions killed male kudus, nyalas and warthogs, and cheetahs killed male reedbucks at greater than expected frequencies. Male nyalas were also killed by cheetahs at high frequencies, though it was not statistically significant (Table 28). Numerous studies have demonstrated a higher rate of predation on male ungulates compared to females (Hirst, 1969; Schaller, 1972; Rudnai, 1974; Fitzgibbon, 1990; Mills, 1990; Ruggiero, 1991; Stander, 1992). Estes & Goddard (1967) believed wild dog predation was associated with the site fidelity of territorial males. Conversely, Walther (1969) believed that in Grant's gazelles, non-territorial males were mostly killed. However, unlike many other bovids, the three species in which males were killed disproportionately at Phinda do not maintain breeding territories (Jungius, 1971; Anderson, 1980; Owen-Smith, 1984) nor do warthog males (Mason, 1982). Fitzgibbon (1990) demonstrated that cheetahs killed more male Thomson's gazelles because they were less vigilant than females. I did not examine vigilance behaviour in any of the species in which males were disproportionately killed. However, in impalas and wildebeest, females were generally more vigilant than males when they were accompanied by juveniles but male impalas looked more than females without young, and male wildebeest and females without young looked the same amount (Chapter 8). Kudu, nyalas, reedbucks and warthogs all differ from these species in generally having small family groups with no territories. Most of them (kudu, nyalas and warthogs: occasionally reedbucks) form small bachelor groups or are often solitary as males. This may increase their vulnerability as they do not have benefit of the 'many eyes' effect which suggests that as group size increases, there are more eyes watching for predators which enhances the likelihood of detection (Lima, 1995). Studies of vigilance, grouping patterns and other predation avoidance behaviour in different social groups (which may vary considerably) of these species would be valuable. It would be particularly fruitful to compare these behaviours where predation pressure is absent or low, and where it is high (see Chapter 8).

Finally, a comment on methodology used for feeding studies of large carnivores is appropriate. I combined data from three different methods of data collection (direct observation, radio-location observations and ranger reports) which as Mills (1992, 1996) had indicated, must be done with caution. Some methods are more likely to increase the contribution of large kills in food habit studies and therefore, pooling data may lead to inaccurate conclusions. The situation at Phinda was different from Mills' study in that lion groups were generally small which increased the chances of all methods locating smaller kills. Furthermore, direct observation was far less effective than in Mills' study site due to dense vegetation and I could not conduct continuous long-term night watches as he and others (Stander, 1992; Hanby *et al*, 1994; Scheel & Packer, 1994) have done in more open habitat. Conversely, as I located all cats usually daily or every second day, my data from radio-location observations probably included more small kills than less frequent telemetry. Finally, while ranger reports were most akin to Mills' opportunistic method (which is known to under-represent small kills), rangers often spent extended periods following lions hunting, recording kills as they happened and so, probably increased the percentage of small kills included. Accordingly, while all three methods inevitably over-represented large kills, there was no difference in the degree to which they did and hence, I pooled the data. As Mills (1992) has discussed, where it can be shown that data from different methods is compatible, combining data may be a useful technique for presenting a more accurate picture of carnivore food habits. The constraints and advantages in the present study are similar to those experienced by many research projects in southern Africa. While thick vegetation may limit the opportunities for direct observation, high levels of tourism activity can significantly supplement data collection. Researchers can improve data collection by being cognisant of such logistical conditions before embarking on a project and by incorporating them in its planning stages.