

CHAPTER FIVE

JACKAL FORAGING ECOLOGY

Introduction

Jackals (*Canis* spp.) are possibly the most common of the larger carnivores in Africa and some parts of Asia, yet they have not attracted the attention of biologists as much as the rare social carnivores, i.e. lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*) and wolves (*Canis* spp.) (Lamprecht, 1981). Since the use of food items by jackals varies with location and time in response to spatial and temporal variation in food availability (Bothma, 1971; Rowe-Rowe, 1983; Hiscocks & Perrin 1987), site- and time-specific investigations are necessary to accurately describe local jackal foraging patterns. Very few investigations of jackal diets have been conducted in Botswana (Smithers, 1971; McKenzie, 1990) and none were specific to southern Botswana, let alone Mokolodi Nature Reserve where they occur as the **only major mammalian carnivore**.

Black-backed jackals are typically described as opportunistic predators, capable of exploiting a wide range of prey depending on local availability (Wyman, 1967; Lamprecht, 1978a; Moehlman, 1978; Rowe-Rowe, 1986). Optimal foraging theory predicts that as the availability of a particular resource (in this case food) decreases, niche breadth (utilisation of that resource) should increase (Krebs & Davies, 1984). This would imply that a species would include more prey species in its diet in areas of lower productivity or if food becomes progressively scarcer in a given area.

Studies on the interactions between social carnivores and their prey species have resulted in useful insights into the evolution of group formation, cooperative hunting, and optimal foraging (Packer & Ruttan, 1988). Such studies often involve an examination of correlations between grouping patterns and hunting success. The type and dispersion of food eaten by members of a species exert an important influence on the social organisation of African ungulates (Jarman, 1974; Underwood, 1982), primates (Clutton-Brock & Harvey, 1978), and carnivores (Kruuk, 1972; Kleiman & Eisenberg, 1973; Mills, 1978). There are,

however, far too few scientific data on the impact of the jackals on prey populations. Fundamental research needs to be initiated to obtain a better understanding of the functional role that jackals play in ecosystems.

A number of methods, both direct and indirect, can be used to investigate the diet of a carnivore (Korschgen, 1971; Mills & Mills, 1978). The most effective one depends on several factors such as the habits and size of the animal, the nature of the study area and the funds at the disposal of the researcher. A study area such as MNR makes it very difficult and laborious to collect direct observational data on foraging habits of black-backed jackals. Satisfactory results are difficult to obtain, especially on smaller food items. This is more so given that black-backed jackals become quite wary and secretive whenever humans persecute them. Hence analysis of black-backed jackal faeces might show the extent to which livestock and small game species are represented in jackal diets. Scat analysis therefore provides a valuable back up as a means of identifying certain food items that were not identifiable from direct observations, and also as a means by which comparisons can be made.

This chapter reports on the foraging/feeding ecology of black-backed jackals at Mokolodi Nature Reserve, Botswana.

Methods

Black-backed jackal foraging ecology was investigated using two main methods: 1) Direct observations; 2) Indirect observations; i) analysis of faecal material, and ii) analysis of stomach contents of jackals killed during problem animal control operations in farms surrounding MNR.

Direct Observations

Direct observations of jackal behaviour were hampered to a large extent by the pronounced human avoidance behaviour of the jackals, probably precipitated by apparent persecution by man as was evident in the areas surrounding the reserve. Throughout much of the present study, flight distance of jackals exceeded 50 m although closer approach could be

achieved within MNR at night. In addition, the rugged terrain coupled with dense vegetation did not allow off-road navigation by vehicle, whilst it was also extremely difficult to follow the jackals on foot due to the dense *Acacia* thickets. Hence it was difficult to employ the focal animal technique exclusively.

Black-backed jackal foraging behaviour was studied during 786 hours of focal animal observations (Altmann, 1974) and also opportunistically. Individual jackals bearing radio collars and ear tags were observed from distances of 50-450 m using 10 x 50 binoculars. Foraging behaviours of other jackals encountered during focal animal sampling or during routine censuses were also recorded. Prey types and sex of prey organisms (wherever applicable) were recorded whenever possible. Observations lasted 1-230 min before the animal was lost to sight. All hunting and feeding attempts, both successful and unsuccessful were recorded. Signs of jackal predation within the park were found by combing through areas where female antelopes had been located with lambs, and also opportunistically during other data-gathering activities.

Reports of jackal predation on livestock from herdsmen and farmers necessitated that observations also be conducted outside the park. Alleged jackal attacks on livestock were investigated at kraals whenever they were reported.

Scat Analysis

Jackals' feeding habits were determined through the analysis of 237 scats collected in MNR from November 1995 to February 1997. Seasons were defined according to jackal breeding biology (see Chapter Four). Faecal analysis is a useful technique for a basic description of a carnivore's diet, particularly where other types of observations are impossible or where time does not permit detailed observations (Korschgen, 1971; Bowland & Perrin, 1993). It is also quite useful in dietary studies of secretive nocturnal animals like black-backed jackals. Furthermore, this technique does not require the sacrifice of the study animal. Faecal analysis may thus be used as a primary or supplemental source of information on animal feeding habits.

Collection

Fresh scats were collected within MNR along paths, roads and opportunistically in other areas. Old scats that appeared to have been defecated in a previous season were not used as samples for the subsequent analysis. All scats around settlements where domestic dogs were common were omitted from analysis. During the study it was notable that jackal pups regularly defecated around the dens although adults were not observed to do so. Faecal pellets at dens were also much smaller in size than faecal material collected elsewhere. I therefore assumed that all faeces collected at dens belonged to pups and that faeces collected elsewhere belonged to adults. Scats were stored in numbered paper bags with the date and position of collection determined by GPS. Each scat was dried at 60°C to constant mass for storage. Since it is possible for seasonal and temporal factors to influence the diet of a predator, the number of scats of the recommended sample size should ideally be collected within a season and in a particular area to enable the accurate determination of the carnivore's diet.

Despite the voluminous information available on the diets of predators, the minimum number of scats required for analysis has not been determined for most carnivore species (Mukherjee, Goyal & Chellam, 1994). Hence, 50 scats were randomly chosen, individually washed over a sieve to remove soil, and oven-dried at 60°C to facilitate handling. This was done to thoroughly mix all the hair and other indigestible remains in the scat. Since it is impossible to analyse every hair in the scat, from the 50 scats, 20 scats were randomly chosen to estimate the minimum number of hairs required for detecting all prey species represented in each scat. As a conservative estimate, Mukherjee, et al. (1994) recommended a minimum of 20 hairs per scat of the Asiatic lion. Henschel & Skinner (1990) also found that 25 scats per month were found to be adequate for analysing hyaena scats. In the present study, percentage occurrence of prey species in the scats of jackals was constant above 30 scats. Therefore a minimum of 30 scats per season was deemed sufficient for estimating diet.

Identification of Prey Items

In the laboratory faeces were sterilised at 110°C for 2 to 4 hours to kill the ova of microorganisms. During analysis, dry scats were weighed, soaked in water and 4% formalin for 12-24 hours with occasional stirring and then rinsed with water over a series of sieves (mesh openings of 3.36, 2.0, 0.6 and 0.25 mm) and then air-dried. This was done to thoroughly mix all the hair and other indigestible remains in the scat. Constituents of each scat sample were then examined under magnifying glasses and a binocular dissecting microscope (2-12.5 X). Food items were then sorted out and identified to the lowest possible taxon. Hair remains were compared with known hair samples.

In addition, detection of mammalian food was based on identification of hairs. Diet was quantified using presence or absence of prey such that equal weight was given to hairs ingested in small amounts. Hairs recovered from scats were identified using published keys (Keogh, 1979, 1983; Buys & Keogh, 1984) and a specially prepared reference collection. Data was recorded as the presence or absence of each prey species in a scat using reference material (mounted hair sections and photographic material of hair sections and the actual mammalian hair collections), housed at the Mammal Research Institute, University of Pretoria. This reference collection contains material of most South African mammals (Bothma & le Riche, 1994.) Some material was sent to specialists particularly at the Transvaal Museum for further analyses.

Hairs were cleaned in absolute alcohol then rinsed in water and air-dried. Scale patterns were obtained from impressions of hairs placed on a slide in a film of coloured 5% gelatin solution. Slides were allowed to cool at room temperature before removal of the hairs. Cross sections were made by placing cleaned hairs in a short, 4 mm internal diameter plastic tube, sealed at one end (Douglas, 1989). Tube and hair were then placed in a test tube containing molten wax (75% paraffin wax and 25% commercial depilatory wax) and returned to an oven heated to about 90°C for 24 hours. Thereafter the tubes were cooled at room temperature. Sections were cut with a sharp scalpel on a sectioning stand (Douglas, 1989) and then glued onto a microscope slide. Macroscopic examinations of prey remains were conducted on hair width and medulla width, texture, colour and banding patterns. In microscopic examination a

combination of hair characteristics such as medullary pattern, other than cuticular characteristics alone was employed in the analysis.

Percentage occurrences of nine broad categories of food were recorded: mammals, birds, reptiles, invertebrates, fruits, vegetable matter, scavenged items, unidentified items, and soil. Small mammalian, and other small vertebrate remains in scats were identified from teeth, jaw fragments, skulls and other bone fragments, and hairs. Avian remains were identified by claws, beaks, and feathers (Bowland & Perrin, 1993). Seeds of fleshy fruits were identified by comparison with known specimens (Rowe-Rowe, 1983; Lindstrom, 1994). Vegetable materials other than fruits were classified as 'Vegetation'. Anthropogenic food items were identified from the presence of curiosities (bone chips, plastic, paper, and string) and undifferentiated matrix (Doncaster *et al.*, 1990). This category was underestimated if processed foods (off-the-bone meats, pure fat, and potato chips) were eaten. Other food items possibly missed by faecal analysis included apples (*Malus* spp.) from which the seeds were left uneaten.

Stomach contents

Stomach contents from 7 jackals killed during problem animal control operations in various farms adjacent to MNR were examined and identified based on the relative frequency of occurrence. Notes on the general condition of the animals were taken where possible.

Animals were examined post-mortem either fresh or after storage in a deep freeze. The jackals were weighed, the gut discarded, and the stomach was stored in 70 % alcohol prior to examination. Obviously, most jackals were killed when some stomach contents had been digested. It was therefore impossible to record volumes or weights of individual food items.

For examination, each stomach was opened and the contents emptied into a white enamel dish. The stomach contents were then washed through a 710 micron wire sieve and immersed in water. Species identification was initially possible in a few cases when the remains of a whole 'small' prey item were present. Otherwise identification of other prey items followed that described under 'Scat analysis'.

Results

Direct Observations

Jackal foraging behaviour was categorised into gathering, hunting and scavenging (Lamprecht, 1978a). Gathering is defined as a type of foraging behaviour, in which food items located by random or non-random search need only be consumed. Food normally obtained in this way consists of relatively small items that cannot escape or evade being eaten by a predator, e.g. fruits.

For the purposes of the present analysis, 'hunting' is defined as a means of acquiring food items, which are either able to escape or to fight back when intercepted by the predator. Hunting thus involves pursuing, catching, and subduing the prey organism concerned. 'Scavenging' here is distinguished from its colloquial use of searching for refuse near human habitations, even though it cannot really be distinguished from gathering small food items in other areas. Typical scavenging in the present context refers to eating from a sizeable prey which had been killed by disease, another predator, an accident, or any other mortality agent, other than the particular jackal under observation. The crux of this rather vague term for the present purposes is that a scavenger eats prey, which would otherwise have required a considerable hunting or searching effort (Lamprecht, 1978a).

Jackals were observed foraging during 37.1% of 786 hours of focal animal observations (including 62.9% of those in which the jackal was foraging when the observation began) and opportunistically in many other instances. It is quite evident that jackals strayed from their territories to devour fresh kills or carrion elsewhere. Hunting accounted for 76.0% ($n = 355$) of all foraging observations. Scavenging was observed 43 (9.2%) times, while gathering accounted for 14.8% ($n = 69$) of all feeding observations. Jackals were observed attempting to kill prey on 355 occasions (Table 11), successfully killing and eating prey on 101 (28.5%) occasions. Of all feeding instances, 21.1 % were kills of rodents. Catches of rodents accounted for 36.6% ($n = 45$) of all successful hunting attempts.

Table 11. Food items eaten by black-backed jackals during direct observations at MNR for the period November 1995 to February 1997

Prey Type	Hunting		Scavenging	Gathering	Total Feeding	% of all feeding observations
	Not Successful	Successful				
Impala	9	3	3	-	6	2.8
Steenbok	2	-	-	-	-	-
Ungulate afterbirth	5	3	-	3	6	2.8
Cape hare	1	-	1	-	1	0.5
Scrub hare	13	5	1	-	6	2.8
Mongoose	3	1	4	-	5	2.3
Rodents	102	37	8	-	45	21.1
Donkey	-	-	12	-	12	5.6
Sheep	1	1	2	-	3	1.4
Goat	3	2	2	-	4	1.9
Game birds	15	2	3	-	5	2.3
Poultry	1	1	3	-	4	1.9
Invertebrates	66	41	-	-	41	19.2
Wild fruits	-	-	-	29	29	13.6
Cultivated crops	-	-	-	7	7	3.3
Anthropogenic scraps	-	-	-	19	19	8.9
Unidentified prey items	33	5	4	11	20	9.4
TOTAL	254	101	43	69	213	

During patrols along roads and tracks, jackals made some incursions into nearby shrubs and long grass searching for potential prey. It was during such explorations when jackals

sometimes flushed their prey, (e.g. rodents, scrub hares, and concealed lambs), which immediately fled. Jackals attempted to catch scrub hares in 13 of 18 instances where hares were flushed. In only 5 of the 18 observed hunts were the hares killed and devoured.

Potential animal and plant food available to jackals varied throughout the year because of its seasonal character. I did not measure prey abundance systematically, but in general, it was apparent in the field that invertebrates at MNR conformed to the general tropical seasonal pattern, with arthropod numbers and biomass peaking in response to vegetative productivity during wet conditions, whilst rodents peaked during the dry season. The two exceptionally good rainy seasons experienced during the study period resulted in huge numbers of both arthropod and rodent prey during the two respective seasons. Most ungulates dropped their young between November and January at MNR. Estimates of ungulate numbers in jackal territories were difficult to determine especially in summer, as was jackal group size because of the difficulty of viewing jackals for extended periods during this season. However, an assessment of the early 1997 stocking rates for mammalian herbivores in MNR are presented in Table 12 (M.R. Greig, unpubl. data).

Jackals at MNR foraged in pairs for most of the time, normally spread out over several hundred metres and covering considerable portions of their range either walking or trotting. Jackals foraging in this manner usually maintained contact by calling or howling. Patches with abundant prey such as rodents and insects were carefully investigated by each of the pair. On several occasions jackals at MNR were observed to walk amongst herds of large wild ungulates and livestock in open grasslands with high rodent densities, moving in zigzag formation presumably foraging for afterbirths or to ambush rodents out of their holes, probably using the herd as a mobile shield (Sillero-Zubiri & Gotelli, 1995) against their prey and their human enemies.

Table 12. Population estimates of large herbivores in Mokolodi Nature Reserve, April 1997

Herbivore Species	Numbers in MNR
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Selective grazers

Impala, <i>Aepyceros melampus</i>	35-40
Eland, <i>Taurotragus oryx</i>	30-35
Hartebeest (Red), <i>Alcelaphus buselaphus</i>	35
Hippo, <i>Hippopotamus amphibius</i>	2
Warthog, <i>Phacochoerus africanus</i>	50-60
Mountain reedbuck, <i>Redunca arundinum</i>	10-15
Ostrich, <i>Struthio camelus</i>	16

Bulk grazers

Gemsbok, <i>Oryx gazella</i>	20
White Rhino, <i>Ceratotherium simum</i>	6
Waterbuck, <i>Kobus ellipsiprymus</i>	15
Zebra (Burchell's), <i>Equus burchelli</i>	25
Elephants, <i>Loxodonta africana</i>	4 (subadults)

Browsers

Bushbuck, <i>Tragelaphus strepsiceros</i>	4
Giraffe, <i>Giraffa camelopardalis</i>	14
Steenbok, <i>Raphicerus campestris</i>	ECC
Klipspringer, <i>Oreotragus oreotragus</i>	ECC
Grey duiker, <i>Sylvicapra grimmia</i>	ECC

NB: ECC denotes those species that have been left to attain 'ecological carrying capacity' in MNR.

Stalking, followed by pouncing on unsuspecting prey on all fours was also displayed as an aspect of foraging behaviour. The extent to which different hunting methods were employed varied according to the size of the prey and the individual hunter (or pair's) skills. Apart from feeding incidents on large carcasses and other clumped food resources (e.g. refuse dumping sites), jackals were located as a group of four individuals on one occasion at the '100' waterhole drinking together. Whether they were or had been foraging as a group at that time was not clear, although they could have been searching for refuse at the chalets next to the waterhole. However, the group disbanded within 15 min.

Pairs of *C. mesomelas* usually approached herds of female impala presumably searching for concealed lambs. Jackals then inspected such areas, sniffing at high grass and shrubs. When nothing could be found, the jackals trotted away to another area where searching was continued. During antelope lambing periods, pairs of jackals moved among female herds presumably inspecting them for signs of lambing. Mostly, the jackals waited until the female had given birth and then worked as a team; one of the pair distracting the female, while the other attacked the young (see Chapter Six). On the one occasion when a pair of jackals encountered a lamb within the herd, the adult impala rescued the lamb by charging the jackal. Both jackals gave way and trotted off. Of the three observed occasions when lambs were flushed out of seclusion in the absence of the mothers, two were successfully killed by a pair of jackals and subsequently disembowelled. Feeding then ensued at a fast rate until they were satiated, whereupon the remains were, in both cases, carried into the nearby bushes presumably to be cached. The other incident was unsuccessful because the single jackal had difficulty in subduing the lamb, whereupon its mother, who was feeding nearby successfully defended it within seconds of the attack.

I also had the opportunity of observing some fascinating jackal predatory behaviour on both domestic and wild ungulates. These interactions were between black-backed jackals and females of parturient impala and livestock (cows *Bos indicus*, and goats *Capra hircus*). As jackals moved among female herds, presumably inspecting the latter for signs of lambing, they also fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In fact, in two instances involving impala and a single case involving a nanny goat, the jackals attacked when these ungulates were lying down calving, particularly during

contractions in the recumbent position (see Chapter Six). In such instances the partly born calf is eaten and the vulva of the mother may also be chewed, with the result that the injured animal ends up being killed by the farm owner. Goats and sheep were the most targeted animals in this case, but circumstantial evidence indicates that cows (*B. indicus*) and other larger wild ungulates were also likely targets.

In addition, informal reports from farmers indicated that injuries inflicted on domestic stock in this manner were a common occurrence in the area during calving periods. Mostly, parturient females were targeted, but even females not in labour were sometimes attacked in a similar manner as evidenced by vulva injuries to those animals that managed to escape and return to kraals.

Jackals were reported to kill stray adult sheep and goats on farmland outside the park boundary, although such predation on adult animals was rarely successful. Herdsmen in the tribal grazing lands reported two sheep and three goats that had been attacked by jackals. Inspection of wounds inflicted on animals which survived attacks revealed typical jackal attack behaviour (Rowe-Rowe, 1986) for the two sheep and one juvenile goat. However, feral dogs could well have savaged the other two goats, although the evidence was not conclusive. Three attacks by jackals on kids were recorded. Location of these was made possible with the assistance of herdsmen. Typically there were neck bites on the carcass (Rowe-Rowe, 1986). Only on one occasion was a jackal observed attacking and subduing a young sheep. The lamb was partially disembowelled during feeding. Thereafter the jackals then tore off chunks of meat, which were carried away into the reserve. Jackals were twice observed feeding on donkey carrion. Such large carcasses were visited many times by several (1-4) jackals, which sometimes also carried lumps of carrion away, presumably to feed pups at dens.

Jackals carried chunks of livestock carrion from the surrounding farming areas into the reserve where it was devoured at leisure. A single male goat carcass was found within MNR. Judging from the large size of the goat carcass, it was probably killed by a leopard (or died of other causes) which dragged it into the reserve where it was fed upon. In another incident, a mangled goatskin was also found at a deserted jackal den. It was impossible to conclude whether the skin was scavenged or a result of predation. Six remains of poultry in the form of

feather clusters were also found at various sites within the park, albeit it was not possible to determine whether they had been killed after straying into the reserve, or were predated upon outside.

There are few observations from which useful generalisations can be drawn on the subject of jackals preying on small livestock (goats, sheep, etc.) and small game (e.g. steenbok *Raphicerus campestris*, impala, etc.). To begin with, jackal kills are often indistinguishable from those of other wild predators and domestic dogs. Moreover, it has been noted that most healthy ungulates living in the same locale as jackals are able to defend themselves against single jackals, so that instances of such predation are rare and hence difficult to observe. The few data that do exist indicate that two or more jackals are usually required to take down, say, a healthy impala adult. In most cases jackals appear to kill either young ungulates or weak ones, typically by attacking the head, lower neck, belly, and rump.

Non-target species such as birds, especially francolins (*Francolinus* sp.) and helmeted guinea fowls (*Numida meleagris*), scrub hares (*Lepus saxatilis*), and mongooses (Family: Herpestidae) caught in traps were most often found to have been retrieved either by jackals, brown hyaenas (*P. brunnea*), leopards (*P. pardus*) and even banded mongooses (*M. mungo*), as was indicated by examination of spoor. Black-backed jackals were also observed caching freshly caught prey on five occasions and retrieving caches on two occasions. Two rodents were cached whole, whereas only remains of one impala lamb, one scrub hare, and a chunk of ungulate carrion were cached. Prey was cached some distance away from the kill. Caching involved digging a shallow hole in a concealed place, usually under some shrubs, and covering the food with soil and/or vegetation. All caches that were observed took place after a jackal had eaten at a kill, usually within 10 min.

Male jackals regurgitated food to respective lactating female partners and young at the den on three occasions. Only one instance of a subordinate jackal regurgitating food at the den was recorded. This behaviour pattern usually occurred after successful foraging. In the pair with no helpers, both members of a pair left the den unguarded to forage on two occasions, but most of the time they alternated, one of the parents (usually the female AFJ1) remaining at the den with the pups. Regurgitating food is an efficient way for adults to transport and

share food. It enables the lactating mother to stay with her pups during their most vulnerable period. This is also beneficial in cases where the level of intra- and interspecific kleptoparasitism is high. Food is much safer within than carried conspicuously outside where it can be misappropriated by other predators or scavengers. Typically, jackals fed on a kill first, and then made off with chunks of meat in their mouths.

The main drawback of the direct observation method was that I was unable to identify many small food items from a distance where normal jackal foraging behaviour could not be disrupted.

Scat analysis

A total of 237 scats, representing 518 items were selected and analysed. Seasonal relative frequencies of occurrence of prey remains in jackal faeces are presented in Table 13 and Table 14. Smaller animal prey species (e.g. rodents and invertebrates) were virtually eaten complete, for fragmented crania, mandibles, teeth, feet, tails, as well as hairs and scales were all found in scats. At least 26 mammal species, 5 bird species, 8 fruit species, and several invertebrate species were recorded as food items of jackals at MNR.

Across all seasons, mammals were the most common food resource (32.4%, $n = 518$; Table 13), followed by anthropogenic items (14.8%), fruits (12.9%), invertebrates (10.8%), birds (8.5%), unidentified items (3.5%), and reptiles (1.4%). Vegetation (8.8%) and soil (6.9%) represented potentially non-food remains. Small mammals (mostly rodents) comprised 39.9 % ($n = 168$) of all mammalian prey remains, wild ungulates accounted for 18.5%, while domestic mammals and medium-sized mammals comprised 15.5% each. Unidentified mammalian prey represented 10.7% of all mammalian prey remains.

Table 13. A summary of the seasonal relative frequency of occurrence of prey remains (%) in 237 black-backed jackal scat samples collected in the Mokolodi Nature Reserve from November 1995 to February 1997. n = number of scats; N = number of specific prey items

Prey category	All Seasons (n = 237)		Summer 1995-96 (n = 38)		Autumn 1996 (n = 53)		Winter 1996 (n = 58)		Spring 1996 (n = 54)		Summer 1996-97 (n = 34)	
	N	%	N	%	N	%	N	%	N	%	N	%
	Mammals	168	32.4	42	31.3	23	25.8	38	41.8	29	30.9	36
Birds	44	8.5	10	7.5	4	4.5	6	6.6	13	13.8	11	10.0
Reptiles	7	1.4	1	0.7	1	1.1	3	3.3	1	1.1	1	0.9
Invertebrates	56	10.8	21	15.7	8	9.0	5	5.5	10	10.6	12	10.9
Fruits	67	12.9	31	23.1	13	14.6	2	2.3	4	4.3	17	15.5
Vegetation	46	8.8	10	7.5	8	9.0	7	7.7	14	14.9	7	6.4
Anthropogenic items	76	14.8	8	6.0	19	21.3	24	26.4	12	12.8	13	11.8
Unidentified items	18	3.5	4	3.0	3	3.4	3	3.3	6	6.4	2	1.8
Soil	36	6.9	7	5.2	10	11.2	3	3.3	5	5.3	11	10.0
Total # of prey items (ΣN)	518		134		89		91		94		110	

Overall, animal prey remains accounted for at least 53.1% of all prey items found in scats, while fruit remains represented 12.9% of all prey items. This relationship was also found in all seasons. Seasonality of prey occurrence in scats was pronounced for small mammals, miscellaneous fruits and invertebrates: Small mammals (mostly rodents) were more frequently eaten in the dry season ($\chi^2 = 48.22$, $d.f. = 1$, $p < 0.01$) and fruits during the wet season ($\chi^2 = 98.09$, $d.f. = 1$, $p < 0.001$; Table 14). All other prey remains occurred in similar proportions regardless of season (Tables 13 & 14).

Table 14. A detailed presentation of the seasonal occurrence of prey items in 237 black-backed jackal scats collected in Mokolodi Nature Reserve for the period November 1995 to February 1997. N = number of specific prey items.

MAMMALIA (N= 168)

Prey remains	Summer 1995-96	Autumn 1996	Winter 1996	Spring 1996	Summer 1996-97	All seasons
	N	N	N	N	N	ΣN
<u>Ungulates</u>	<u>10</u>	<u>3</u>	<u>3</u>	<u>8</u>	<u>7</u>	<u>31</u>
<i>Taurotragus oryx</i>	1	0	0	1	0	2
<i>A. melampus</i>	4	0	1	3	2	10
<i>Tragelaphus strepsiceros</i>	2	1	1	1	0	5
<i>Equus burchelli</i>	1	0	0	0	1	2
<i>Phacochoerus aethiopicus</i>	1	1	0	1	3	6
<i>Raphiceros campestris</i>	0	1	1	2	0	4
Unidentified	1	0	0	0	1	2
<u>Medium-sized Game</u>	<u>3</u>	<u>6</u>	<u>5</u>	<u>3</u>	<u>9</u>	<u>26</u>
<u>Mammals</u>						
<i>Lepus capensis</i>	0	1	2	0	1	4
<i>L. saxatilis</i>	1	2	2	2	4	11
<i>C. mesomelas</i>	1	0	0	0	3	4
<i>Genetta genetta</i>	0	2	0	1	1	4
Unidentified	1	1	1	0	0	3
<u>Small Mammals</u>	<u>19</u>	<u>9</u>	<u>22</u>	<u>10</u>	<u>7</u>	<u>67</u>
<i>Mungos mungo</i>	2	1	1	0	1	5
<i>Saccostomus campestris</i>	3	2	2	0	0	7
<i>Rattus rattus</i>	2	0	3	3	1	9
<i>Rhodomys pumilio</i>	4	1	4	2	1	12
<i>Aethomys namaquensis</i>	1	2	2	1	1	7

<i>Tatera</i> sp.	0	1	2	1	0	4
<i>Galerella</i> sp.	1	0	1	1	0	3
<i>Otomys angoniensis</i>	1	1	3	0	0	5
Unidentified	5	1	4	2	3	15
<u>Domestic Mammals</u>	<u>4</u>	<u>2</u>	<u>3</u>	<u>5</u>	<u>12</u>	<u>26</u>
<i>Capra hircus</i>	2	1	0	3	6	12
<i>Ovis aries</i>	1	1	2	1	3	8
<i>Equus</i> sp.	1	0	1	0	3	4
<i>Bos indicus</i>	0	0	0	1	1	2
<u>Unidentified mammals</u>	<u>6</u>	<u>3</u>	<u>5</u>	<u>3</u>	<u>1</u>	<u>18</u>
<u>N =</u>	<u>42</u>	<u>23</u>	<u>38</u>	<u>29</u>	<u>36</u>	<u>168</u>

AVES (N = 44)

<i>Pterocles bicinctus</i>	1	0	1	1	0	3
<i>Struthio camelus</i>	2	1	0	2	1	6
<i>Francolinus</i> sp.	3	0	2	1	1	7
<i>Numida meleagris</i>	1	3	2	3	1	10
Egg shells	0	0	0	2	3	5
Unidentified	3	0	1	4	5	13
<u>N =</u>	<u>10</u>	<u>4</u>	<u>6</u>	<u>13</u>	<u>11</u>	<u>44</u>

REPTILIA (7)

Lacertidae	1	1	1	1	0	4
Unidentified	0	0	2	0	1	3
<u>N =</u>	<u>1</u>	<u>1</u>	<u>3</u>	<u>1</u>	<u>1</u>	<u>7</u>

INVERTEBRATA (N = 56)

Coleoptera	1	1	1	2	2	7
Orthoptera	10	3	0	1	4	18

Myriapoda	2	0	0	0	1	3
Scorpionida	0	1	0	0	1	1
Hymenoptera	2	1	0	1	0	4
Isoptera	4	2	3	5	2	16
Unidentified	2	0	1	1	3	7
N =	21	8	5	10	12	56

FRUITS (N = 67)

<i>Grewia</i> spp.	11	7	1	1	6	26
<i>Ximenia caffra</i>	4	0	0	1	3	8
<i>Ziziphus mucronata</i>	3	0	0	0	1	4
<i>Sclerocarya birrea</i>	2	2	0	2	1	7
<i>Zea mays</i>	6	1	0	0	3	10
<i>Malus</i> spp	3	2	1	0	2	8
Unidentified	2	1	0	0	1	4
N =	31	13	2	4	17	67

VEGETATION (N = 46)

Twigs	3	2	1	3	1	10
Dicot Leaves	3	4	2	6	1	16
Monocot Leaves	4	2	4	5	5	20
N =	10	8	7	14	7	46

ANTHROPOGENIC ITEMS (N = 76)

Bone chips	2	4	7	1	1	15
Plastic	0	2	3	2	0	7
Paper	0	1	1	1	0	3
String	0	0	1	0	0	1
Bottle tops	1	2	1	0	0	4
Fish remains (bones & scales)	2	1	3	1	3	10
Poultry remains	1	4	2	3	5	15

Cultivated fruit seeds	0	1	0	0	1	2
Cloth	0	0	2	0	0	2
Leather	1	0	0	1	0	2
Rubber	0	2	1	2	0	5
Unidentified	1	2	3	1	3	10
N =	8	19	24	12	13	76

UNIDENTIFIED ITEMS (N = 18)

N =	4	3	3	6	2	18
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SOIL (N = 36)

N =	7	10	3	5	11	36
ΣN	134	89	91	94	110	518

On an aggregate level, the seasonal pattern of use of mammalian prey was rather constant, with a moderate decrease during autumn (Table 13), but these differences were not statistically significant (T-test: $t = 5.7$, $p = 0.055$). Impala (*A. melampus*) comprised the bulk (32.3%, $n = 31$) of ungulate scat remains, followed by warthogs (*Phacochoerus africanus*) (19.4%), and kudu (*Tragelaphus strepsiceros*). Remains of impala and other medium-sized ungulates were probably a consequence of lamb mortality partially precipitated by jackal predation as is suggested by results from direct observations. Neonatal ungulates are vulnerable to mortality agents at or shortly after birth, but they quickly outgrow this vulnerability. It is most likely that large ungulate remains were scavenged as carrion or fresh kills of other carnivores such as leopards (*Panthera pardus*). Medium sized prey accounted for 15.5% of all mammalian prey, and these were mostly represented by scrub hares (*Lepus saxatilis*) (42.3%, $n = 26$), followed by Cape hares (*Lepus capensis*) and small spotted genets (*Genetta genetta*) in similar proportions of 15.3% each. Jackal hair remains (15.3% of medium-size mammals) were probably a result of (allo)grooming, although intraspecific predation on young (and feeding on jackal carrion) is not a remote possibility (Moehlman, 1983). Domestic mammal remains were represented by sheep (*Capra hircus*) (66.7%, $n =$

18), goats (*Ovis aries*) (44.4%), donkeys (*Equus* sp.), and cattle (*Bos indicus*) (4.5%) remains. Most small mammalian preys were terrestrial, crepuscular and nocturnal, and inhabitants of Acacia savanna woodland and grassland, whereas few species (e.g. *Otomys angoniensis*) were predominantly diurnal. Other animal preys were largely diurnal. As previously noted in Chapter Four, jackal activity periods in MNR closely coincided with that of its prey, in addition to the relative activity of humans.

The crested guinea fowl (*Numida meleagris*) represented 22.7 % (n = 44) of all avian remains, whereas ostrich (*Struthio camelus*) and francolins (*Francolinus* sp.) accounted for 13.6% and 15.9%, respectively. Invertebrate remains were represented by the exoskeletons of ants (order: Hymenoptera), dung beetles (order; Coleoptera), grasshoppers (order; Orthoptera), termites (order; Isoptera), millipedes (order; Myriapoda), and scorpions (order; Scorpionida). The Isoptera were mostly represented by harvester termites *Hodotermes mossambicus* (which were the most abundant and more often consumed prey item during the dry season), *Trinervitermes* sp., and the mound-building termite *Macrotermes* sp.

Two types of anthropogenic food items were identified in the scats. First, remains from domestic animals typified by white chalky faeces containing abundant poultry claws, feathers and bone chips, and fish remains (e.g. fish scales and bones) resulting from the activities of anglers who operated in the nearby rivers and dams. The second type, derived from feeding on exploitable scraps from refuse disposal sites or garbage bins, typified by dark brittle faeces containing plastic bags, bottle tops and fragments of glass, together with some commercial fruit pips (e.g. apples *Malus* sp. and oranges *Citrus* sp.). Remains of domestic mammals were however classified under the general 'Mammals' food item category, while remains of locally cultivated crops (e.g. maize *Z. mays*, melons and squashes) were included under 'Fruits'.

'Fruits' included seeds of *Grewia* spp., large sourplum (*Ximenia caffra*), buffalo thorn (*Ziziphus mucronata*), melons and squashes (Family: Cucurbitaceae). Single seeds of marula trees (*Sclerocarya birrea*) were also retrieved from scats. Jackals usually rested under the shade of marula trees and fed on the fruits which had fallen to the ground. Usually the pulp was ingested whilst the hard seed was spat out, but these were sometimes swallowed. Exosperm remains of maize (*Z. mays*) were also found in jackal scats. It is unclear whether

these fruits were eaten for their energetic content or moisture content, but individuals were observed to eat, and then drink at waterholes. The fruits of *Grewia* spp. were eaten throughout the year by jackals except when the parent plants were in flower.

Stomach contents

The sample for stomach contents was unevenly distributed throughout the year since animals used were obtained from problem animal control operations which were naturally biased to the winter season when jackals were most often intercepted by hunters and trappers.

Table 15. Percentage occurrences of food items found in stomachs of black-backed jackals in Mokolodi Nature Reserve and surrounding areas

Food Item	No. of Stomachs	Percent occurrence (%)	Relative percent occurrence (%)
Game carrion	2	28.6	4.3
Livestock carrion	3	42.9	6.4
Other carrion	3	42.9	6.4
Artiodactyla	2	28.6	4.3
Sheep	2	28.6	4.3
Goats	1	14.3	2.1
Rodentia	3	42.9	6.4
Aves	1	14.3	2.1
Invertebrates	5	71.4	10.6
Cultivated crops	1	14.3	2.1
Unidentified mammals	4	57.1	8.5
Vegetation	4	57.1	8.5
Anthropogenic items	3	42.1	6.4
Soil	6	85.7	12.8
Unidentified items	7	100.0	14.9

Analysis of 7 jackal stomachs revealed an array of prey organisms (Table 15). Dipteran larvae were found in some stomachs, thus indicating that jackals also fed on carrion in addition to live prey. Carrion (game and livestock) accounted for 17.0% of all prey items in stomachs. Invertebrates were the most common single prey item occurring in 71.4% ($n = 7$) of all jackal stomachs, and this represented 10.6% of all prey items found in stomachs.

Discussion

Direct Observations

Jackal predatory behaviour on ungulates observed in the present study is of particular note because although jackals may be small relative to most wild and domestic ungulates, they have nonetheless perfected their predatory behaviour to be capable of causing substantial losses to ungulate herds through natal mortality. The injuries inflicted on the vulva of parturient females is also important, particularly in domestic stock where the injured animal usually ended up being killed, sometimes in addition to the loss of its young to jackal predation. Such behaviour clearly underlines opportunistic predation by jackals, usually depicted in the variety of prey items taken, but also in the modes of food acquisition under varying ecological circumstances. Jackals have also been reported to scavenge on wildebeest (*Connochaetes taurinus*) afterbirths in the Serengeti plains (Jarman, 1976) and have been implicated in causing similar injuries to cows (*B. indicus*) in labour (Skead, 1973). The killing method used in the subjugation of ungulate young is typical black-backed jackal killing behaviour; neck and head bites aimed at severing the trachea and suffocating the prey (Rowe-Rowe, 1986). Of special note is the apparent selection of neonatal impala by jackals, since these were some of the least common age group of the population. However, this could also be due to the inability to detect neonatal impala by the investigator, relative to jackals.

Jackals changed their diets when prey species became vulnerable to predation. For example, impala lambs were most vulnerable when less than two weeks old. Jackals took advantage of this vulnerability, as field observations suggested. When jackals were feeding mostly on small prey, group size was smallest consisting of single individuals. Jackals do not

need to hunt together when preying on rodents, fruits, reptiles, or insects, and one jackal does not benefit from the small prey that another has caught. When large prey were intercepted, pairs and sometimes groups of three individuals cooperated in bringing the animal down. Larger jackal groups were both evident in summer and winter, but these were seldom observed to hunt cooperatively. Possible mechanisms driving the increase in jackal group size and subsequent change in foraging ecology may be increased sociality among pack members during the breeding season and delayed juvenile dispersal (Gese, Rongstad, & Mytton, 1988; Moehlman, 1986). The interplay between group size and prey size is presented and discussed in Chapter Seven.

In black-backed jackals, pair-hunting may be an adaptation to overcome hunting problems: lambs are often defended by their mothers, and a pair of jackals can more easily cope with the double task of catching the lamb and warding off its mother (Eaton, 1969; Lamprecht, 1978a). Pair hunting may also considerably offset the competitive pressure, as two jackals can eat a lamb much faster than one, thus lessening the risk of kleptoparasitism. In MNR however, such a situation may not predominate presumably because potential large carnivore competitors do not exist apart from the rare brown hyaena and the occasional leopard. However, intra- and interspecific kleptoparasitism cannot be completely ruled out since observations revealed that trapped non-target species were retrieved by predators other than jackals, in addition to observations of caching behaviour which suggests the presence of competition. A jackal family in possession of a carcass (either killed or scavenged) can exploit it more fully than a single individual. I have observed single jackals at carcasses spending most of the time threatening vultures rather than feeding, and occasionally being driven away by vultures. Thus the feeding ecology of black-backed jackals involves not only availability, distribution, and size of food items, but also intra- and interspecific competition to retain and consume food. In addition, the high level of hunting pressure around the MNR area would select for rapid feeding on kills outside the reserve to avoid detection by humans. Under such circumstances it would also benefit jackals if kills outside the park were brought within where they could be consumed in a relatively safer environment. The fact that remains of a number of domestic species were found in the reserve partly serves to support the jackal foraging behaviour described here. However, transportation of food into the park would also involve the risk of being detected or being dispossessed of the kill by other kleptoparasites. We would

therefore expect the animal to 'trade-off' between feeding on the site of the kill and transporting to an area of safe feeding, according to the local ecological setting.

Although cooperative hunting has previously been invoked to account for large group size in most social predators, its general application is somewhat misplaced. It is often thought, mistakenly, that the terms 'hunting group' and 'social hunting' imply the wholesale adaptation of all such units to cope with big and/or fast prey animals, i.e. that they are invariably adapted to the requirements of the hunt. But in the case of black-backed jackals in MNR, this only rarely seems to be the case. Where it does apply, hunting groups tend to consist of only two or three individuals. Bigger groups more often seem to be adapted to problems arising only after a successful hunt, e.g. competition with kleptoparasites for the kill. In fact, sometimes the groups seem to be adapted to problems quite unconnected with hunting and feeding, such as protection from intraguild predators, kleptogamy, and even competing for territories, but which nonetheless compel animals to live together (Lamprecht, 1978b; 1981). Besides, some overlap of group home ranges, especially at crucial areas such as watering holes or in the vicinity of carcasses, has been observed for this species in which the groups are normally mutually exclusive (Rowe-Rowe, 1982; Ferguson, Nel & De Wet, 1983; Moehlman, 1983, 1986).

Scavenging may also be seen as an added dimension that gives those carnivores that practice it the potential to increase far beyond the bounds imposed on pure predators. However, not every scavenging carnivore succeeds equally. A classic example in African savannas is that epitomised by the rare striped hyaena (*Hyaena hyaena*) and the relatively common spotted hyaena (*Crocuta crocuta*). Success demands on exactly the right combination of attributes; a species with antisocial, retiring habits, which is largely restricted to habitats with limited food resources, obviously will not be as successful as a gregarious one utilising a variety of habitats. Hence it must be their ability to exploit scavenging to the limit, added to their abilities as predators, that accounts to the numerical ascendancy of black-backed jackals and spotted hyaenas in much of sub-Saharan Africa.

The senses of black-backed jackals in MNR that facilitate the location of prey are most probably the following (in decreasing order): olfactory, visual, and auditory, but this may

vary according to the nature of the habitat and prey being sought. In MNR where visibility is limited by dense woodland vegetation, olfactory cues may definitely predominate over sight, whereas sight would be more important in open grasslands. This is of particular adaptive importance for hunting cryptic prey such as impala lambs, which are usually hidden by their mothers for the first few days after parturition (see Chapter Six). Furthermore, olfactory cues are quite important in woodland habitat for avoiding humans where hunting pressure is high. This was clearly manifest in the difficulty of trapping jackals during the present study. When prey are visible, pursuit based on visual cues is most likely to start before olfactory or auditory cues can come into play, but when prey are well-hidden, jackals probably rely on some combination of olfactory and auditory cues. The exact combination probably depends on the aeolian conditions and the amount of noise made by prey. Jackals are efficient predators and can always switch back and forth between these various hunting modes in order to take maximum advantage of whatever the environmental conditions are at the time.

It must be noted that the risk of predation is an integral part of the foraging behaviour of animals. For example, an animal that has been observed to locate and consume several prey items may be said to be exhibiting foraging behaviour. Surely the animal may have ingested some food, but was it just 'foraging'? Surely this animal must have been 'considering' not only its options as they relate to efficient food intake, but also how those options influence its risk of being preyed upon. To the extent that the term 'foraging behaviour' is associated strictly with the act of food intake, its use in describing behaviour is misleading because it detracts attention from important determinants of behaviour that are unrelated to energy. The same can be said of any behaviour, not only foraging. Furthermore, it is also important to note that the risk of predation does not 'constrain' behaviour. Although it is often stated that the risk of predation acts as a constraint on foraging behaviour (e.g. Krebs & Davies, 1984; Milinski, 1986), one could just as easily argue that foraging is a major constraint on predator avoidance (Lima & Dill 1990). The fact is that neither foraging nor predation act as constraints. The behavioural options open to a feeding animal lie on a continuum between energy maximisation (at the complete expense of predator avoidance) and minimisation of risk (at the complete expense of feeding). Clearly, neither extreme option is desirable and optimal behaviour will lie somewhere in-between. Lima & Dill (1990) suggested that the term, 'constraint' be reserved for factors such as gut size, day length, which are not under the

individual's control and therefore actually constrain the animal to a particular set of behavioural options.

Stomach contents

Although the sample size of stomachs used for the analysis of jackal feeding habits is small ($n = 7$), indications are that the jackals in MNR also scavenge, thus playing an important role by eating garbage and animal carrion in and around towns and villages. The diet is dependent upon the availability of food items and ranges from vegetable matter to ungulate prey. This is not surprising since in Bangladesh, golden jackals (*Canis aureus*) have even been reported to feed on sugarcane and rice stems (Poche, Evans, Sultana, Hague, Sterner & Siddique, 1987).

The consumption of grass is known to be both voluntary and involuntary, possibly aiding in food digestion and to satisfy their vitamin (C) requirements. Smithers (1971) found that green grass occurred in 14 out of 59 stomach contents. In seven of these cases the stomach containing the green grass was empty or nearly empty. Domestic dogs (*C. familiaris*) and cats (*Felis catus*) frequently eat green grass, and this is usually taken when the stomach is empty (pers. obs.). Unlike green grass, dry grass occurred along with other detritus but it is likely that the latter was ingested fortuitously or along with Isoptera or other invertebrates. Grass could also appear in remains or stomach contents if ingested with the alimentary canal of the prey species. Rowe-Rowe (1976) also reported on a jackal stomach that entirely contained grass.

The presence of fly larvae in stomach contents would depend on how long after death the jackal found and fed on the carcass, the time of year that the antelope died, and the portions eaten by the jackal. (Dipteran larvae that were found with mammal remains were not recorded separately as insects). Some of the other antelopes were also eaten as carrion as fly larvae occurred in some stomach contents. Carrion might have been the remains of animals killed by a jackal, but which were too large to be entirely consumed on the day of the kill - or the animal might have died of other causes (Rowe-Rowe, 1976, 1983) Similarly, fresh meat found in the stomach might have been from an animal killed by the jackal, or from an animal

that had died of other causes and had been scavenged by jackals shortly afterwards. Jackals can legitimately be considered as problem animals on sheep farms and other small livestock since they are responsible for the loss of potential income (Rowe-Rowe, 1976; Fair, 1994).

Scat Analysis

Prey occurrences found here are similar to those found in previous studies (e.g. Bothma, 1971; Rowe-Rowe, 1976,1983). As previously stated, jackals changed their diets when prey species became vulnerable to predation. Selection of the neonatal antelopes (e.g. steenbok, *Raphicerus campestris*, and impala, *Aepyceros melampus*) could account for the preponderance of ungulate prey in the wet season scat samples. Impala lambs are most vulnerable when less than two weeks old, and during the present study, jackals took advantage of this vulnerability. Small mammals and murids constituted a major part of jackal diet, particularly during the dry season (winter-spring). In the case of small mammals, while there is no evidence to prove this, it is assumed that the jackal had killed them itself. Remains of springhaas (*Pedetes capensis*) and scrub hares (*Lepus* spp.) were found in scats, but murids constituted a major proportion of the diet. These included *Tatera* sp., *Aethomys namaquensis*, *Saccostomus campestris*, *Rattus rattus*, and the diurnal species *Rhodomys pumilio* and *Otomys angoniensis*.

The presence of poultry remains (e.g. feathers, beaks, and claws) in scats reveals their importance in the diet of jackals and the tendency of jackals to frequent human settlements in search of food. The dietary habits of black-backed jackals in the present study at MNR reveals that, in order to obtain sufficient food, they extended their range from their woodland refuges within the MNR to include human settlements where livestock damage was observed. Refuse dumping sites near human habitation were frequently utilised at night as sites of reliable food sources. It was apparent that rodents (particularly *Rattus rattus*) also occurred at high densities at refuse dumping sites, underscoring the jackals' preference for such rich patches of food. Although wild animals played a considerable part in jackal diet, jackals probably incorporated domestic species into their diets due to reduced availability of their usual wild prey.

Based on faecal analysis jackals undergo seasonal changes in the relative frequencies of animal and plant matter ingested. The seasonal increase in remains of fruits in the faeces of jackals should not necessarily be interpreted as a decrease in consumption or importance of animal matter (Ball & Golightly, 1992). For example, if jackals in the wet season ingested the same number of rodents as in the dry season, and incorporated fruits into their diet, the remains of rodents would be a smaller percentage of all the food remains. It might appear as though fewer rodents had been eaten, and that jackals had changed from a diet of predominantly animal prey to fruit. However, in a study on grey foxes (*Urocyon cinereoargenteus*), Ball & Golightly (1992) found that berries contributed little to protein balance; other sources of protein (animal matter) must be ingested, even if the foxes could consume adequate amounts of berries to meet their energetic requirements. They found that even if a fox ate about 1,6 kg of berries, the small amount of protein in that diet would be inadequate for maintenance and the fox would still have to forage for animal prey. Furthermore, percent digestible and metabolizable energy of a mice diet was significantly greater than that of berries. Digestible crude fat and crude protein were also found to be significantly greater for diets composed of mice than of berries. By extension, an exclusively frugivorous diet can impose a premium on the energetic and nutrient demands of jackals at MNR. Hence, jackals may switch to animal diets in response to increased demands for protein, energy and other nutrients probably as a result of their reproductive activities. In particular, on an aggregate level, in MNR the importance of animal diet for jackals is manifested in the similarity of the frequency of occurrence of mammalian prey remains across all seasons (Table 13), albeit noteworthy differences are revealed at finer levels of resolution (Table 14).

Seed dispersal by jackals probably benefits host species. Fruits, when they are abundant, provide an easily obtainable source of carbohydrates for jackals. Further, fruits are a sessile food resource and grow in patches. Their yearly presence within the home range of a black-backed jackal, given climate-induced fluctuations, is relatively predictable in time and space. Encounters with fruit patches by jackals could occur while searching for animal prey. When a patch is encountered, a volume of berries could be exploited from the plants with relatively little expenditure of energy and/or time, while yielding some energy to the jackal. In areas of restricted fresh water, jackals that consume fleshy fruits may reduce the amount of time they

spend travelling to other water sources. Hence jackals may ingest fleshy fruits more for water content of the fruit than for energy content, especially under moisture limited environments.

Whether the jackals were acting as predators or dispersers of seeds cannot be determined from a study of this type. In order to define the role of jackals in plant reproduction in the area, studies which examine the viability of seeds after passing through the jackals' digestive tract and selection of foods in relation to availability would be required. If seeds were viable after consumption by jackals, some aspects of their behaviour such as the extensive use of roads for travelling and defecating, might enhance its importance as a seed disperser, helping plants to recolonize abandoned roads, old fields, and other clearings due to human extractive activities in the area. On the other hand, these same habits could result in ineffective seed dispersal when faeces are deposited in areas of perpetually high disturbance where seeds have little chance of germinating, such as along the maintained roads, on rocky outcrops, and in the gravel pits. The role of the jackals in plant reproduction in the area merits further investigation due to the relatively high numbers of jackals and their high consumption of fruits.

A striking observation on the potential of jackals in seed dispersal in MNR was noted in the dispersion of *Grewia* spp. plants, whose seeds occurred most frequently in jackal faeces throughout the year. There was a marked difference in the abundance and distribution of *Grewia* spp. within the reserve and in the tribal grazing areas. *Grewia* spp. occurred widely and were well-established within the park, while they were almost non-existent in the surrounding farming areas, save for a few tufts of stems almost browsed to ground level. Repeated browsing by domestic livestock (especially goats) outside the park is likely to account for this difference but I suggest that defecation activities of jackals while marking territory is also likely to have an effect through seed dispersal and subsequent (re)establishment in various localities. This is more likely to be the case since defecation activities were confined to areas of low disturbance such as inside the reserve. This clearly indicates the potential of jackals to contribute to plant reproduction, but still, this merits further investigation.

Birds were a relatively minor part of the diet throughout most of the study. Birds are generally difficult to catch, and jackals have many failures between catches. The peak in bird remains in faeces occurred in spring and summer when ground-nesting game birds were brooding and the population was swollen by chicks, presumably easier prey than adult birds. Their higher mortality also would have made them more commonly available as carrion. Birds also featured strongly in the scat remains in the dry season when their access to vegetative cover possibly was limited. However the interpretation of jackal diet based on game bird (or poultry) plumage remains must be treated with caution, especially when assessing the impact of jackal predation on avian prey. In the red fox, *Vulpes vulpes* it has been found that feathers stay longer in the stomach than smaller plumage and other parts of prey (Reynolds & Aebischer, 1991; Lovari & Parigi, 1995). Therefore it has been suggested that a scat analysis based on micro-fragments should be used to assess the real contribution of birds, which otherwise may be underestimated, to the diet (Reynolds & Aebischer, 1991). On the other hand, after undergoing prolonged digestion in the stomach, feather fragments are presumably passed on through the pyloric sphincter. Thus, smaller plumage and fragmented feathers of the same bird are likely to show up in separate scats, and this would result in an overestimate of the importance of birds in scat analysis (Lovari & Parigi, 1995).

Based on my field observations, I suspect that during the wet season, jackals ingest higher quantities of arthropods than are detected in faeces. Several times I observed jackals feeding on areas heavily infested with caterpillars. These observations suggest that the jackals were primarily eating the larvae and adults, and may have helped reduce damage to grassland and crops inflicted by caterpillars. However, detection of larval remains would be limited by digestion of all soft body parts. In winter the activities of harvester termites (*Hodotermes* spp.) could impact heavily on the relative availability of graze to ungulates and livestock, especially during prolonged drought periods (Kaunda, 1994; J.M. Dangerfield, pers. comm.). Thus the predatory activities of jackals on Isoptera could help reduce 'overgrazing' by termites on pasture and also decrease damage to crops during the harvesting season. Like jackals, aardvarks (*O. afer*) and bat-eared foxes (*O. megalotis*) have also been implicated as allies in the fight against termites and other insect pests (Van Heerden, 1988).

Given the addition of anthropogenic food resources and altered habitats in human settlements, black-backed jackals' diet at MNR was more diverse and differed from that reported in relatively undeveloped areas (Wyman, 1967; Hall-Martin & Botha, 1980; Smithers, 1971; Lamprecht, 1978a; Rowe-Rowe, 1983). Results of observational data and scat analysis reported here indicate that jackals are opportunistic feeders, that eat carrion as well as practically any animal they can easily overpower - a behavioural trait which led Estes (1967) to designate them as 'predator scavengers' as compared to the pure predators ('scavenger predators'). Jackals are highly adaptable animals being able to exist as predators on small game and livestock, scavengers, eat insects or rodents, and as indicated in the present study, also feed on anthropogenic food sources, wild fruits, and agricultural crops. The relative importance of scavenging and predation in the lives of jackals varies according to both time and place. Where large social carnivores and their prey are plentiful, they may live largely as scavengers if they themselves are not too numerous (Estes, 1967). Where pure predators are scarce, as is the case in MNR, they may be very active hunters; in fact they have been implicated to even partially fill a pure predator's vacated niche. Like other predators, jackals behave so as to maximise their fitness, which is often done by maximising their net energy intake. In fact, a predator's prey choice is not only a consequence of prey energy content, but it also depends on the predator's success in finding, handling, and consuming its prey. Other studies on jackals' diet have revealed similar feeding behaviour (e.g. Wyman, 1967; Bothma, 1971; Smithers, 1971; Rowe-Rowe, 1976), albeit with some deviations from the findings of the present study.

There are a number of difficulties inherent in the interpretation of carnivore diets based on scat analysis. Only indigestible material can be recorded so that the consumption of soft tissue from large carcasses without the ingestion of hair would be difficult to detect. It is also impossible to differentiate with certainty between prey that have been killed by the predator and those that have been scavenged. Conversion of items from frequency of occurrence to contribution to the diet of biomass is also liable to severe bias. Large prey cannot be consumed totally at one meal and the remainder could either be eaten at subsequent meals or alternatively by other predators and scavengers. Small items may be consumed totally but the presence of their remains in scats cannot be used to determine how many individuals were represented. Furthermore, small prey containing a relatively higher proportion of indigestible

matter (hair, bones, and teeth) and their remains are over-represented in scats. This makes analysis of diet data involving percentage volume or percentage weight of prey remains in scats biased towards smaller prey. Scats also cannot be identified to individual predators, so that specialist and generalist foragers cannot be distinguished. Interpretation of data based on scat analysis must, therefore, be done cautiously within the constraints of the methodology (Oli, Taylor, & Rogers, 1993; Weaver, 1993). Even with an adequate faecal sample, there are problems with the analysis of the data (Mills, 1992a). The identification of hair is often difficult particularly in species with a diverse diet. Finally, for most prey species it is impossible to differentiate between the hair of adults and juveniles.

The percent occurrence of prey in the diet also gives no measure of the proportion of encounters in which a prey type is ignored. It could be argued that a reduction in the percent occurrence of an item in the predator's diet reflects a reduction in the proportion eaten of that item. This would only be true if densities of each prey item were to remain constant. Otherwise, changes in percent occurrence of an item in the diet could be caused by changes in the density or proportion of other prey eaten. Without relative measures of prey density it is impossible to determine the cause of the change and thus make predictions to test prey choice models. Interpretations of prey choice models are further complicated when prey types differ considerably in size. Changes in the number of large items consumed will have a relatively greater influence on the dry matter ingested than similar changes in the number of small prey consumed. Percent occurrence in the diet must be converted to some index of the actual number of prey consumed to be able to test prey choice models (Boutin & Cluff, 1989).

Finally it is impossible to determine whether food was scavenged or killed by the predator, which is an important consideration, particularly for the jackals (Bowland & Bowland, 1991; Bowland & Perrin, 1993). Although a more realistic measure could be obtained from intestine/stomach contents when digestion of items is not yet completed, faecal analysis is a non-intrusive method of estimating diet, and also provided sample sizes sufficiently large to measure relative changes in composition from season to season without disturbing the population under study (Doncaster *et al.*, 1990).

CHAPTER SIX

JACKAL PREDATION ON IMPALA

Introduction

The impala (*A. melampus*) is an abundant antelope species inhabiting the woodlands and savannas of eastern, central and southern Africa. They are typically found in riverine habitat in the dry season, moving into surrounding deciduous woodland or savanna in the wet season (Jarman & Jarman, 1973; Murray, 1982). Locally, their dispersion may be clumped or irregular, but groups are known to have open membership and no social units other than that of mother and young (Schenkel, 1966; Jarman & Jarman, 1973). A gradual disintegration of the mother-young bond is usually evident in the declining proximity between dam and lamb and the increasing proportion of observations in which lambs associate with peers (Jarman, 1976; Mooring & Rubin, 1991). The formation of peer groups has been seen as one indication of the start of a weakening mother-infant relationship (Lent, 1974; in Mooring & Rubin, 1991). Near the equator, reproduction is not seasonal and births occur throughout the year (Jarman & Jarman, 1974). However, breeding activity in southern Africa takes place during a 'rut' of 3-5 weeks in May-June (Fairall, 1972; Murray, 1982; J.D. Skinner, pers. comm.). Thus breeding is short and synchronised. During the remainder of the year, male impala are found in loose coalitions with other males (bachelor herds) or in herds of mixed sex. Lambs are no longer isolated from the herd with the dam after about the first week (Schenkel 1966; Jarman, 1976; Mooring & Rubin, 1991).

Predation has been offered as a cause of synchronised breeding in ungulates (Estes, 1966; Kruuk, 1972), the advantages being increased predator detection, predator confusion and satiation of predators (Ims, 1990). However, Skinner & Van Jaarsveld (1987) argued that predator swamping must have been preceded by seasonal reproduction, the former just acting to tighten-up the breeding season. Intermittent breeders (Dott, 1987) react to environmental cues (e.g. lunar cycle, Murray, 1982) but predation reduces the breeding period, as young born during the fringes of the calving season have a higher mortality rate (Estes, 1966). Impala react to a shortening day-length and mate in May in order to lamb after the spring

rains, probably to ensure optimal milk production for the young when there is a high quality food source during summer (Skinner, 1989). Rainfall regimes in habitats such as the Kalahari strongly affect vegetative productivity (Van Rooyen, Bredenkamp, & Theron, 1991). In environments in which seasonal climatic changes significantly alter resource availability, reproductive success often depends on the timing of breeding: offspring born late in the breeding season have a lower probability of survival and grow at a slower rate than those born earlier. Synchrony of reproduction with environmental factors ensures that females have access to good food supplies during energetically demanding periods, which for mammals occur during late gestation and lactation.

Predation risk is an important element of the environment influencing animal behaviour, reproduction, and distribution. An individual's risk of predation varies over time and from place to place depending on such factors as the amount of cover, the type of predator, and visibility (Lima & Dill, 1990). In addition, foraging benefits also vary and frequently conflict with anti-predator behaviour, so individuals are forced to 'trade-off' the benefits of foraging against the need to reduce the risk of predation. The ability for prey animals to select their 'enemy-free space' (Jeffries & Lawton, 1984) has evolved as an adaptation under different circumstances of time, habitat, and predator type.

In some mammals, the predation risk level depends on the amount of activity leading to increased visibility, audibility, or smell (Norrdahl & Korpimaki, 1995). A considerable body of evidence suggesting that reproductive activity places animals under increased risk of predation (or fatal parasitism) exists (Lima & Dill, 1990). For example, the risk experienced by males may be increased in several ways, especially by calling and display behaviours conspicuous to both females and predators (reviewed in Lima & Dill, 1990). Although most such cases reported to date deal with insects, the effect is undoubtedly more general. In the case of females, pregnancy may increase predation risk by increasing visibility to predators or decreasing speed and manoeuvrability. One or both sexes may also pay a cost in terms of increased vulnerability to predation often associated with parental duties. Furthermore, as breeding increases activity, noise, and smell, and as olfactory cues are important in breeding, but may be used by predators as cues in hunting, a non-breeding mammal probably has lower predation risk than a breeding one.

For all these reasons, the reproductive period is often a time of greatly increased predation; this is part of the 'cost of reproduction' which influences the evolution of life-history patterns (Stearns, 1976). Given that reproductive activities increase the risk of predation and that animals have made mortality-reproduction trade-offs in evolutionary time, it would be surprising if they did not do so in ecological time as well, i.e. base reproductive decisions on estimates of the prevailing risk of predation. For example, animals may delay reproduction under temporarily high predation risk. If temporarily high predation risk has a suppressive effect on prey reproduction on a large scale, we expect a negative association between predation risk level and the proportion of breeding individuals in prey populations. But animals cannot delay breeding forever, as dying without breeding means a fitness of zero. So, delayed breeding is expensive and should only happen under temporarily high predation risk i.e. there has to be a high probability that predation risk will decrease in future (Korpimäki, Norrdahl, & Valkama, 1994; Norrdahl & Korpimäki, 1995). Thus if mating and reproduction increase the risk of being preyed upon, trade-offs between current reproduction and future survival might result in a temporary reduction in reproductive investment when predation risk is high.

In most studies of jackal predation it has been found that the animals killed by jackals are not a random sample of the available prey population with respect to age, sex, and body condition (e.g. Rowe-Rowe, 1983, 1986; Stander, 1987; McKenzie, 1990). However, the selectivity shown by jackals varies between areas and different prey types, as a result of the inherent vulnerabilities of prey types, environmental conditions, or the spatial distribution of prey (Wyman, 1967; Smithers, 1971; Lamprecht, 1978a; Moehlman, 1978). Selective predation occurs when the relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment (Chesson, 1978a,b). Selectivity for prey types within the principal prey species influences how jackals affect population dynamics of their prey. Although impala are killed by a large range of predators (all the larger felids, canids, and hyaena, as well as baboons (*Papio hamadryas*), bateleur eagles *Terathopius caudatus*, pythons *Python sebae natalensis*, and crocodiles), black-backed jackals are particularly adept at killing impala, especially where the larger social carnivores are absent. Reduced mobility

and alertness of the female during parturition increases her vulnerability to predation at this time and new-born impala become easy prey for black-backed jackals (Schenkel, 1966).

Predation can confound interpretation of vegetation-ungulate relationships because low survival of young can be viewed as an indication of food limitations when actually the population is being limited by predation. However, the general effects of predation on ungulate populations such as impala, are difficult to assess without intensive studies. Furthermore, detailed studies of maternal behaviour in species with precocial young are more difficult to carry out on wild animals than those involving altricial young. This is because close observation is generally impossible without causing disturbance. Detailed behavioural observations are difficult to make from a distance since parturition frequently takes place in an area concealed by vegetation or within a group of conspecifics. However, information concerning the development and survival of newborn lambs is critical to proper management. Since dead neonates are virtually impossible to locate, it has not been practical to appraise directly the extent of these losses. But because this information is needed for sound management, the subject could hardly be ignored however difficult to document. This chapter reports on observations of jackal predation on impala at MNR.

Methods

Observations of jackal predation on impala were conducted through focal animal sampling of jackals during their foraging activities, opportunistic observations, and from routine track censuses. Evidence that an animal was killed by jackals included an obvious chase sequence in sandy areas, signs of a struggle, haemorrhage associated with bite and claw marks, blood splattered on nearby vegetation, distance between canine bites and site of bite (Rowe-Rowe, 1986; Thurber & Peterson, 1993).

Population Size and Composition

Counts of impala in the study area indicated the proportion of lambs, subadults, adult males, and adult females. Counts were conducted along the extensive road network in the reserve especially on rarely driven roads for 2-4 days preferably after rainfall events. The sizes of impala herds and their composition by sex and age class (lamb, adult female, adult male) were determined from all herds seen incidentally during fieldwork. Each recognisable herd was recorded only once per day. Mandibles of impala carcasses were collected for relative age determination from tooth wear, replacement, eruption, or growth (Fuller & Kat, 1990).

During some 40 000 km of driving and walking within the nature reserve, so few animals were seen that it would have been meaningless to attempt a quantitative analysis of road strip counts and other sightings as only small numbers of impala herds were seen within the study area. No attempt was also made to capture and mark impala lambs due to the risk of parental desertion associated with handling by humans. Capturing impala lambs may cause abandonment and subsequent starvation especially given that conspicuous collars, ear markers, and other tags may make marked lambs more vulnerable to predation than unmarked ones. This is much more likely to happen when lambs are only a few hours old and/or when the mother is primiparous.

Habitat Overlap of Impala and Jackals

Ground locations (including telemetry locations for jackals) of impala and jackals were recorded. The vegetation type at each location was recorded to determine habitat use. The locations were assigned to one of seven broad habitat types on the basis of habitat classification of the park (see Chapter Four). Habitat overlap of jackals with the different classes of impala was assessed with the percent overlap measure (Krebs, 1989). Since no lambs were radio-collared, habitat use by lambs and dams was assumed to be the same.

Results

Although circumstantial evidence indicated the prevalence of jackal predation on impala at MNR, direct observations of such predation were quite difficult to document. Dense or closed vegetation structure and the rugged topography did not allow for observations of study animals for extended periods. The secretive nature of the jackal population at MNR also exacerbated this shortcoming. In addition, locating impala proved to be a particularly daunting task since their positions at any particular time could not be readily determined to enable direct observations. This was primarily because they were not radio-tagged in addition to the fact that their areas of utilisation were sometimes inaccessible. Besides, since impala hide their young during the first few days after birth, data on birth behaviour and subsequent neonate mortality could not be documented satisfactorily.

Notwithstanding these limitations, opportunistic observations resulted in the documentation of two noteworthy jackal attacks on parturient impala dams. Jackals probably decoded some behavioural peculiarities of impala in parturition since they were observed to frequent female impala herds during the lambing period. Pre-birth cues such as the unusual position of the tail which was held away from the body and obvious contractions thereafter, while assuming the straining posture similar to the urinating posture, were probably used by jackals to single out females about to give birth. Parturient females that isolated themselves from the herd in preparation for labour were then followed from a distance. Both attacks on impala occurred during labour, the first while the female was in the recumbent position. On the afternoon of 21st November 1996, a pair of jackals attacked a parturient impala dam that had isolated itself from the herd to give birth lying down. The two jackals grabbed the half-expelled foetus, pulled it from the vulva, and killed it instantly by puncturing the head region. The two jackals then speedily consumed the dead foetus by tearing it into two chunks. The mother, which had trouble getting up presumably due to exhaustion, finally managed to stand up and disappeared into some nearby bushes and was lost to sight.

The second interaction occurred during the same summer (16th December 1996), while radio-tracking the family of jackal AFJ1. This altercation involved three jackals and another parturient female impala that had some foetal legs protruding from the vulva but clearly had

trouble isolating from the main herd for seclusion preparatory to imminent delivery. The jackal group in this instance somehow managed to spot the 'unusual' behaviour of the impala. The male of the jackal pair approached the parturient impala, by first sniffing at drops of birth fluids while searching the immediate vicinity. The male jackal was then quickly joined by its female partner AFJ1 and what I judged to be a subadult jackal (presumably the pair's offspring of the previous year). Upon ascertaining the source of the scent the three jackals converged on the parturient impala and attacked it from the rear, the sides, and head region of the impala dam. The other members of the impala herd disappeared into the bushes oblivious to the struggles of the impala under attack. No attempt to mob the marauding predators was attempted. The adult male and subadult jackals grabbed the protruding legs and head region of the foetus from the vulva, while the adult female delivered some bites to the neck and head region. There were some futile attempts to disgorge the foetus from the vulva, and this ended in two of the jackals tearing at the vulva, while the third jackal delivered a suffocating grip on the lower neck of the impala dam. Eventually the clearly exhausted impala dam was overpowered and died on the spot. The whole interaction from attack to eventual subjugation lasted for 27 min. Within a further 20 min of this kill some vultures and one lone jackal had congregated on the kill, which was devoured frantically, in what appeared to be a clear case of intra- and interspecific competition. It is quite plausible that the impala dam was an inexperienced primiparous female, judging from its inability to identify and select a concealed spot for giving birth prior to the appearance of the foetus from the vulva. Except for signs of the kill, no remains of the impala carcass were located on the site the following morning. The carcass or what remained of it, was probably misappropriated by kleptoparasites (leopards or brown hyenas) as revealed by spoor remains.

Impala breeding at MNR was restricted to less than six weeks in November/December, 1996. No breeding out of season was observed. Although two births were observed, it was not possible to obtain enough accurate data to present a complete description of the development of the mother-young bond. It appears that parturient impala dams give birth in isolation presumably under cover of some bush thickets since very small lambs were mostly observed in dense undergrowth. Young impala do not follow their mothers within a few hours (as in wildebeest) or days (as in hartebeest *Alcelaphus* spp. or gazelles *Gazella* spp.) after parturition (Schenkel, 1966; Jarman, 1976). For quite a number of days and during many

hours each day the young is hidden in undergrowth, while the mother remains vigilant in the vicinity. Later, the lamb moves more and more frequently around its mother, but during this period the synchronisation of movement, which appears between mother and young in many ungulates of the open savanna grasslands, was not observed in impala.

Two more impala females showed evidence of similar past jackal attacks as evident from vulva scars during the 1996-97 lambing season. Older concealed lambs were killed by pairs of jackals searching through impala lambing grounds, probably using olfactory cues (see Chapter Five). Whenever the lamb was with its mother, one jackal attempted to distract the mother while the other member of the pair attacked the lamb. In MNR this was observed on three occasions, two of which were successful (Chapter Five), but indications are that such phenomena are more common than appears from these observations for reasons already alluded to previously. Jackals could be found among impala herds ($n = 7$) during the late afternoons and at night during the lambing periods. Although up to three jackals could be observed to take part in a hunt, in general jackals hunted impala lambs in pairs, as described in Chapter Five. Impala lambs were captured due to total exhaustion after persistent attacks, by being bitten under the neck, and then persisting with the pressure. In some instances, impala dams and sometimes the whole herd, tried vigorously to protect their young from jackal attacks through predator harassment with varying degrees of success.

Jackals were observed hunting adult impala other than females in labour and lambs on four occasions. However, none of these were successful, even though in one case, a pair of jackals could not bring down a clearly emaciated adult male impala, even after repeated mock-attacks. I documented adult impala in MNR charge and chase jackals on five occasions. Four of these cases involved impala dams while one involved members of a bachelor herd. Three of the chases by impala dams involved individual lone females while the other involved the whole herd with lambs among them. No lone males were observed to be involved in predator harassment, presumably due to the risk involved in singularly intercepting a potential predator.

Despite the paucity of direct observations of jackal attacks on large mammalian prey, it is plausible that the presence of fresh lamb remains (e.g. portions of legs or hooves) found

scattered at certain sites within MNR could have signified jackal predation or other mortality factors although such evidence remains inconclusive (also refer to the discussion under Chapter Six). This was apparent during late November and early December 1996. In total, nine signs of impala lamb kills at different sites were identified from remains of body parts within the reserve, six of which were associated with jackal modes of killing. These remains were found scattered over what appeared to be impala lambing grounds or areas where lambs may have been concealed. In particular, observations from some of the farming properties next to MNR (Lion Park and Brink Estates) where there were relatively larger resident populations of impala, the situation was so severe that numerous leg-portion remains could be found literally strewn over known impala lambing grounds. However, it was not possible to undertake a direct quantitative appraisal of jackal predation in these areas, although this may have shed some more light on the nature and extent of jackal predation in such environments.

Most causes of lamb mortality were difficult to determine in MNR because remains of lambs (when there were any) were located a long time after the lamb's death and were badly mangled and had begun to decompose. Frequently, only lamb remains in the form of uneaten portions of legs were found. Either these were also eaten as part of the kill or immediately scavenged by other predators or scavengers e.g. brown hyaenas (*P. brunnea*), mongooses (Family: Herpestidae), bateleur eagles (*Terathopius caudatus*) and Cape vultures (*Gyps coprotheres*). Hence complete information was not obtained on every specimen. No lamb carcasses were found intact apart from those few instances when jackals were directly observed feeding on freshly killed lambs. Remains of impala lambs were mostly found within jackal home ranges, which closely corresponded with those of female herds. Impala dams had greater habitat overlap with jackals than did males (Table 16).

Table 16. Habitat use by impala in Mokolodi Nature Reserve and habitat overlap with radio collared jackals.

Proportional use of habitat by:			
Habitat type	Male Impala	Female Impala	Black-backed Jackals
Short thorn savanna	0.39	0.26	0.21
Tree and bush savanna	0.21	0.36	0.42
Open savanna grassland	0.01	0.02	0.03
Seasonal floodplain	0.07	0.10	0.10
Semi-sweet mixed bushveld	0.18	0.15	0.13
Riparian woodland	0.14	0.11	0.09
Croton/Combretum tree savanna	0.00	0.00	0.01
% Overlap with jackals	70.3	88.8	

The number of herds incidentally seen during fieldwork and the average size are presented in Table 17. Most impala encountered were members of bachelor herds, while female herds, usually accompanied by a single male harem-holder, were encountered less often. Lambs and herds of mixed composition were particularly rarely encountered.

Three juvenile male impala were injured by predators (presumably by leopards or feral dogs), but nevertheless survived the attacks as shown from bite marks over their bodies. Fresh carcasses of two more yearling male impala, one adult male, and an adult female, were located in MNR during the present study. None of the carcasses could be connected to any particular mortality factor, apart from the yearling male impala that had a fractured limb which could partially be attributed to jackal predation as indicated by signs associated with jackal killing methods. This yearling impala carcass was later found on two occasions being devoured by groups of 2-4 jackals and some vultures.

Table 17. Composition of the impala population, the relative numbers of herds of each class, and their average size

Sex-age class	Number of times herds were seen	Mean Size of herd	Proportion
Males > 1yr	19	5 (range = 4 to 7)	0.48
Females > 1yr	11	16 (range = 10 to 22)	0.29
All Lambs	4	6 (range = 3 to 9)	0.10
Mixed herds	5	12 (range = 7 to 19)	0.13

Most carcasses were so old that collection of femur for the analysis of the Bone Marrow Fat Index (Depperschmidt, Torbit, Alldredge, & Deblinger, 1987; Shackleton & Granger, 1989; McKenzie, 1990) would have been impractical. However, whenever possible, skulls were collected for relative age determination. While it would have been desirable to augment these data by shooting some proportion of the impala population in MNR, this was not done because of likely disfavour from reserve management especially given their concern for the dwindling impala population.

On an individual basis, lambs and male yearling impala appear to be slightly selected for, while adult females are strongly underrepresented. Because males show less habitat overlap with jackals, they are encountered proportionately less often, and the observed kills probably represent a slightly higher selectivity for males upon encounter. On a herd basis, however, both adult classes are underrepresented and lambs are strongly over-represented. There are fewer males than females in the population, but because females are in larger herds, numbers of male and female herds are almost equal. Lambs occur in far fewer herd equivalents, because they make up a small proportion of the dam-lamb herds in which they are found. This results in fewer expected encounters with herds containing lambs, and the number of lamb kills represent strong selectivity for lambs upon encounters with herds.

Discussion

Although evidence of black-backed jackal predation on impala was difficult to obtain, information garnered from the present study was quite indicative. The fact that jackals were found to predate on neonatal impala as well as on yearlings and emaciated or senile adults indicates jackal potential to limit impala population increase in MNR, particularly through natal recruitment. The impala population in MNR has been estimated at 35-45 individuals, and at least 22 of these were females (pers. obs.). The findings of the present study indicate that two impala lambs were directly observed being killed and devoured by jackals, while another two died at foetal stage before expulsion from the parturient dams' vulvae. In addition, six lamb remains found in MNR during the 1996-97 lambing period alone, were attributed to jackal predation, yielding a total of at least 10 impala lambs killed that season. Given that each female impala gives birth to a single lamb per breeding season, and assuming that half of the impala dams had successfully conceived, it becomes evident that jackals in MNR may be limiting the population growth of resident impala. At a conservative estimate, overall, at least half of the annual calf crop (approx. 25% of the total impala population) fell prey to jackals during that season alone. The number of impala lambs that succumbed to jackal predation therefore constitutes a significant proportion of the impala population, and in conjunction with other natal and adult mortality factors, can considerably limit, or rather depress population levels.

A number of studies of predation on ungulates have demonstrated selection for lambs and calves (e.g. Mitchell *et al.*, 1965; Lipetz & Bekoff, 1980; Stander, 1987; the present study), while in other studies calves were taken in proportion to their abundance, or selectivity changed seasonally (Rowe-Rowe, 1975, 1976; Fuller & Keith, 1980; Lipetz & Bekoff, 1980). Similar selectivity for young and old animals has been found in studies of predation on white-tailed deer, though selectivity for calves was not always apparent (Huggard, 1992). Selectivity for calves may also be stronger when the prey species is more abundant (Huggard, 1992). Local fluctuations in lamb survival rates may also be attributed to changes in predator density, abundance of alternate prey, and vegetation production and its impact on female impala nutritional status (Huegel, Dahlgren, & Gladfelter, 1985)

During the breeding season, adult impala seem to be in little danger of predation by jackals since impala lambs present during the lambing period are more susceptible to predation than adults. However, jackals may prey on adult impala at other times, e.g. during the dry season. Selectivity for calves when they are available is expected, as they are generally slower, less dangerous, and inexperienced with predators. In a study of predation by a switch of predators on large mammalian prey in Kafue National Park, Zambia, Mitchell, Shenton, & Uys (1965) found that predation was heavy on the juvenile group, reduced on yearlings, whilst the sub-adult groups were hardly taken at all, undoubtedly due to the vigour and alertness of the subadult age-group. Mitchell *et al.*, (1965) reported that predation (by lions *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, and wilddog *Lycaon pictus*) on antelope lambs and calves on average accounted for 27.9% of large mammal deaths. The sex ratio of large mammalian prey was male biased (1: 0.85, n=470). Impala prey sex ratio was also particularly skewed with a ratio of 1 male: 0.5 females (n=18). In moose, adult males were selected over adult females in some systems (Fuller & Keith, 1980), while females were selected in others (Ballard *et al.*, 1981, in Huggard 1992). In other areas either no selectivity is found or the selected sex may change seasonally (Messier & Crete, 1985).

Neonate Concealment

The main antipredator behaviour used by the young of many bovids and cervids is to hide (FitzGibbon, 1993). The mother and infant are only in contact for short periods and infants rely on cryptic coloration and minimal activity to avoid detection by predators. The success of the hiding behaviour depends on the mother minimising the transmission of information concerning the lamb's presence (Byers & Byers, 1983). Otherwise, predators searching for hidden lambs could use this information to increase their chances of success. As most predators hunt visually, isolation from the herd and concealment would act to reduce possible predation on mother and young. While a mother can merge, behaviourally and physically, with other herd members, the anti-predator benefits of herding apply. However, as soon as she differs from them she is relatively more at risk from predators (the 'oddy effect' - Lima & Dill, 1990) and concealment becomes a more profitable strategy (Jarman, 1976). The importance of this behaviour is indicated by the very strong urge to isolate even

when harassed persistently by a territorial male attempting to keep parturient females within the herd. It appears that impala lambs fall between a pure-hider and a pure-follower strategy, while the mother-young bond is weak and ephemeral. Observations of wild impala have shown that offspring do not preferentially associate with the mother after weaning at 4-6 months, but instead associate most with age-mates (Murray, 1981). New-born impala have been reported to show a strong and initially unspecific following response (Jarman, 1976): In fact, new-born impala which happen to be near other impala frequently attempted to follow individuals (or any moving object) other than their mothers and tried to suckle from strange females and even males.

The time available for the formation of the mother-young bond may be limited. It is well known that domestic goats will reject their newborn young as early as one hour after birth (pers. obs.). Similar behaviour has been observed in sheep (Jarman, 1976). Basic behavioural similarities between impala, sheep (*Ovis aries*), and goats (*Capra hircus*) suggest that such cognate behavioural patterns also exist in impala. The development of mobility by the young impala in the first half hour after birth adds to the danger that if the mother-young bond is not well-established soon after birth, the young may either be rejected by the mother, or if it is temporarily separated from its mother, it may not be recognised when relocated. Impala females are known to only suckle their own offspring; orphans still dependent on milk are rejected by other lactating females and die of starvation (Jarman, 1976). Lack of isolation from conspecifics could easily delay the formation of the mother-young bond. As most impala females stand up from time to time while giving birth, the preferred bush clumps were considerably more effective as shields than the long grass or shrubs used by other females. Too thick bush areas or too long grass could be detrimental as mother and young need to maintain visual contact in the first hour, particularly while the following response is unspecific. It was apparent that most females were unsuccessful in isolating and concealing themselves and reliance on this alone as an anti-predator device would be precarious. Newborn impala are particularly vulnerable to predators in the first hour after birth (Jarman, 1976); the following response is not yet specific to the mother and they tend to scamper away from her as soon as they are mobile. Consequently, giving birth in the middle hours of the day presumably allows several hours for the development of the mother-young bond before predators become active at dusk.

Placentophagia

Jackals are known to feed on ungulate afterbirths, but the extent to which this behaviour pattern occurred in MNR was quite noteworthy. The fact that impala dams usually eat their own placenta immediately after the expulsion of young at birth could predispose them to jackal attacks as soon as signs of imminent birth appear. Although the motive (from the jackals' perspective) may primarily be to feed on the placenta, the fact that the incidence of placentophagia is immediate for impala may necessitate early attacks by jackals, which could eventually lead to the death of the partially-born foetus, and injury or even certain death to the mother too. It has been reported that in some cases, impala in labour even start consuming their birth membranes and cleaning birth fluids even before the foetus is completely delivered (Jarman, 1976). Thus a jackal foraging for impala afterbirth would benefit from attacking the parturient female before the latter feeds on the after-births or placenta itself.

Placentophagia and the consumption of all birth fluids in impala may act to reduce predation by removal of attractants for predators such as jackals that have acute olfactory senses. Wildebeest also exhibit placentophagia but whereas the time from birth to expulsion is variable for impala, in wildebeest expulsion is delayed for at least three hours (Estes, 1966; Jarman, 1976). This has an obvious advantage for wildebeest, as it allows the calf more time to gain co-ordination before the expulsion of a placenta, which in many instances was eaten by jackals or vultures who homed in on it almost immediately. Presumably, the anti-predator behaviour of concealment in impala, which is a reasonable possibility in their relatively more wooded habitats, reduces the advantage gained by delaying expulsion (but not for long), and this behaviour in wildebeest is part of a complex of adaptations to existence in open country. However, as evidenced by jackal attacks on parturient impala in the present study, it appears that the hiding strategy and the promptitude of the onset of placentophagia seldom pays dividends for impala since black-backed jackals have apparently perfected a versatile 'counter-strategy' to circumvent such a situation.

Although most senses of the black-backed jackal are acute, their sense of smell is exceptionally well-developed (Skinner & Smithers, 1990). In particular, Skinner & Smithers (1990) reported an instance of a single jackal seen following up the downwind scent of a dead springbok in the open plains of Botswana from a distance of well over a kilometre! Such sensory acuity does not bode well for impala reproduction in dense habitats such as in MNR because although impala mothers can hide their lambs, the well-developed sense of smell of jackals probably enables the latter to eventually locate and kill hidden lambs. Hence, even with relatively dense vegetative cover, predation by jackals may be intense during the hiding phase of impala lambs. Besides, although lambs may be relatively safe from predation during the early 'hiding' phase, the onset of flushing age at about 2 weeks heralds another episode of enhanced vulnerability of lambs. Predation could be severe during this transition period when there is vulnerability and lambs are more active and detectable but still catchable (Nelson & Woolf, 1987; Kunkel & Mech, 1994). Hence in areas of relatively elevated jackal densities, neonate mortality may considerably limit population increase. In the present study, sample sizes for lamb mortality were however too small to make strong inferences from such data. Further research is needed to determine whether neonate mortality is compensatory or additive and how this affects impala population dynamics. It is however plausible that wherever jackals and impala are sympatric it is likely that some level of predation whether on lambs or adults is bound to occur; however the extent and nature of predation may vary among areas and among years within an area.

The individuality of behaviour of impala females during parturition was very striking, particularly in the reaction to and early care of the newborn. The behaviour of the females which may have been primiparous indicates that some mother-young behaviour may be learned, and an experienced mother may improve the young's chances of survival by helping it to suckle and by cleaning up the birth fluids and membranes more quickly and efficiently than primiparae do (Jarman, 1976). There are strong selection pressures operating at this time for the accomplishment of isolation, concealment, and parturition in a minimum of time at the right time of day. Any variation in behaviour may influence the survival of both the mother and young.

Habitat Structure

Discussions of predator-prey relationships have often focused on the direct effects of reduction in prey abundance due to predation. However, other less direct effects of predation pressure have also been recognised. These include behavioural modifications that result in shifts in habitat usage and changes in foraging activity (Kennedy, Shave, & Spencer, 1994). In the presence of a predator, foragers must choose between a loss in foraging time through engaging in avoidance and escape behaviours or a potential loss in resource availability through a shift to a predator-free habitat. Optimal foraging models have been used as a way of examining how the presence of a predator affects the behaviour of prey species (Krebs & Davies, 1984; Lima & Dill, 1990). Any change in the ability to discriminate among the relative profitabilities of sites can affect the forager's distribution among those sites (Dukas & Ellner, 1993). The poorer the information available to the foragers the more likely they are to choose randomly among the sites and consequently become vulnerable to predation. As the change in behaviour coincides with the addition of a predator into the foraging environment, it is reasonable to assume that the predator's presence causes the change in the forager's behaviour. Animals may, therefore, alter their behaviour as a trade-off between perceived danger and food intake rate (Krebs & Kacelnik, 1991).

For example, most African antelopes avoid cover which might obscure and/or harbour predators; for these animals cover is not only a refuge, but also a source of risk (Underwood, 1982). In particular, impala generally occur in bush and mixed habitat which led Fuller & Kat (1993) to surmise that this made them relatively easier to fall prey to predators such as wild dogs in dense habitat. Vegetation density may also affect the survival of neonatal impala because increased cover may reduce predation for predators that rely primarily on visual cues to locate prey, e.g. aerial predators (Moreno, Villafuerte, & Delibes, 1996), especially during the first few days when lambs are most sedentary. The reduced size of exposed areas tends to reduce the chance for foraging predators to detect their prey. But carnivorous mammals such as black-backed jackals are primarily stalkers, relying on auditory and olfactory, in addition to visual cues, to detect and capture their prey in shrubs and bushes. By extension, dense vegetation, which characterised much of impala habitat utilisation in MNR, may also be a

high-risk habitat for impala. Hence, habitat structure can determine prey availability as well as prey vulnerability (Corley, Fernandez, Capurro, Novaro, Funes, & Travaini, 1995).

In the case of impala at MNR familiarity with the area was tantamount to breeding success especially with respect to the selection of calving grounds free from core jackal activity or even outside the predators' home ranges. Interestingly in the present study, female impala habitat utilisation overlapped that of jackals to a greater extent, and it was apparent that most impala lambing areas were effectively within jackal home ranges. Since the recognition of mammalian predators by their prey could be based on olfactory cues, we would expect prey to be able to 'decode' the carnivore scents used for territory marking, individual and intersexual recognition (Jedrzejewski, Rychlik, & Jedrzejewska, 1993) to avoid core predator activity centres for improved prey breeding success. However, this may not be the case in MNR because selection of sites relatively free of predators may be difficult in such a relatively small, physically circumscribed area.

The Effect of Herds

The spatial distribution of male and female impala may also be proposed as a factor generating increased predation on yearling males, which tend to be found on the periphery of preferred areas, where they are more likely to be encountered by predators, especially at the height of the rut (Skinner & Smithers, 1990). A similar effect may explain the bias towards young males in predator kills. Male juvenile impala remain with their mothers until the rut in autumn of their second (yearling) year, at which time the harem-holding male chases the yearling males to the fringes of his territory, while female yearlings remain in the breeding herd. Yearling males in this study were often observed at the edges of larger herds in autumn. Peripheral individuals are the first to be encountered when predators attack an impala herd, and naive male yearlings are likely to be particularly vulnerable during these encounters.

During the lambing season (late spring/early summer) impala usually occur in small bull herds and larger dam/lamb herds (Estes, 1995). Animals in herds can see and hear others in the herd and all react to danger together. Increased wariness by impala after an attack probably makes them less vulnerable to subsequent attacks by jackals. Charnov *et al.* (1976)

have termed this effect 'behavioural depression'. The detected presence of a predator may increase alertness of the prey and temporarily depress prey availability. An increased alertness of impala following an attack by jackals causes the jackals to move to another area. In the present study, jackals moved throughout their territory and did not remain in individual areas of high (impala) prey density, and the kills were distributed more uniformly than the prey. Such patterns indicate that kills cannot be made repeatedly from one herd. Females may be underrepresented compared with males because females usually occur in herds with young that are preferred by jackals. When jackals encounter a female herd, they are more likely to attack the young, and the alerted females become less vulnerable to predation. Males generally do not have the benefit of lambs to divert such predation. From this herd-based point of view, males are not necessarily more vulnerable or preferred than females. They are encountered proportionately more by jackals because they occur in small, and therefore relatively numerous herds, and do not benefit by associating with calves. Lambs, though preferred by jackals, are not highly selected for overall because they occur in fewer herds.

Because little to no detailed information is available on the interrelationships between jackals and prey prior to the increase in modern man's influence on wildlife and habitats, the character of that relationship under pristine conditions remains to a large degree speculative. As human encroachment and agriculture continue to reduce wildlife habitat in Botswana and other parts of the world, management decisions must be founded on a precise understanding of wildlife ecology and population dynamics. In particular, one important aspect of ungulate ecology is the extent and causes of lamb mortality. Although it is usually impractical to eliminate or even reduce the major factors in lamb mortality, an understanding of these factors is necessary to further our understanding of herd dynamics and improve the predictive capabilities of wildlife managers (Kunkel & Mech, 1994). Although the general effects of predation on ungulate populations are difficult to assess without intensive studies, monitoring prey with radio telemetry is a more direct method of measuring losses to predation. Collaring dams and lambs for prompt relocations of dead and live animals as indicated by radio signals (mortality sensors) can provide better tally of losses to predation or other mortality factors, thus improving diagnostic opportunities.