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PREY SELECTION AND FEEDING HABITS OF THE LARGE CARNIVORES IN THE SOUTHERN KALAHARI

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Abstract – Prey selection and feeding habits of lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*, cheetahs *Acinonyx jubatus* and leopards *Panthera pardus* are investigated. Lions kill mainly adult gemsbok *Oryx gazella* and blue wildebeest *Connochaetes taurinus*, tending to select older animals of both species and males in the case of gemsbok. Spotted hyaenas also prey mainly on gemsbok and wildebeest, but select for juveniles, particularly from gemsbok. Cheetahs prey heavily on springbok *Antidorcas marsupialis* lambs and then on adult males and older individuals. Leopards also prey relatively heavily on springbok, but appear to have a wider diet than cheetahs do. It is concluded that predators generally have a small impact on their prey populations in the southern Kalahari, although in the case of springbok they do appear to influence the structure of the population.

Introduction

This paper investigates prey selection and feeding habits of lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*, cheetahs *Acinonyx jubatus* and leopards *Panthera pardus* in the southern Kalahari. The two other large carnivores found in the area are excluded, either because they are so rare: wild dogs *Lycaon pictus*, or because they are almost exclusively scavengers: brown hyaenas *Hyaena brunnea* (Mills & Mills 1978).

Although studies on the feeding habits of each individual species have, or are, being conducted in the southern Kalahari — lions by Eloff (1973a, 1973b), cheetahs by Labuschagne (1979), leopards by Bothma and Le Riche (*in press*) and spotted hyaenas by Mills (*in prep.*) — to date none of these authors have accumulated large samples of prey of known sex and approximate age over an extended period, nor have they obtained data on the population structure of the prey. This is necessary when questions such as ecological separation between the carnivores and their impact on prey populations are being addressed.

Numerous similar studies have been undertaken in other African reserves (Wright 1960; Mitchell, Shenton & Uys 1965; Kruuk & Turner 1967; Hirst 1969; Pienaar 1969; Schaller 1972). The inherent dangers in extrapolating this type of information from one area to another, justifies a similar type of study in yet another area, as it is important from a management point of view to assess the role that predation plays in the ecology of different areas.

Study area

Most of the material was collected in the Kalahari Gemsbok National Park, Republic of South Africa, with some coming from the areas immediately adjacent to the Nossob riverbed in the neighbouring Gemsbok National Park, Republic of Botswana.

The area is semi-desert with a mean annual rainfall of approximately 240 mm. It is largely covered with a layer of red wind-blown sand piled into dunes. The dunes are broken by two dry riverbeds which flow through the area from the north-west and by some irregularly distributed large pans. The vegetation is an extremely open shrub or tree savannah.

The major ungulate species of the area are gemsbok *Oryx gazella*, springbok *Antidorcas marsupialis*, blue wildebeest *Connochaetes taurinus*, red hartebeest *Alcelaphus buselaphus*, eland *Taurotragus oryx*, steenbok *Raphicerus campestris* and common duiker *Sylvicapra grimmia*. All except the last two mentioned species are to a greater or lesser degree nomadic, depending on ecological conditions, although there are always some springbok, gemsbok and wildebeest in the area (Mills & Retief 1984). Ostriches *Struthio camelus* and large rodents such as porcupines *Hystrix africaeaustralis* and springhares *Pedetes capensis* as well as hares *Lepus* sp., are common and widespread, as are black-backed jackals *Canis mesomelas* and bat-eared foxes *Otocyon megalotis*.

Methods

All the data for lions, leopards and cheetahs, and some for spotted hyaenas, were obtained when carcasses were fortuitously located by myself and other field staff, between 1974 and 1982. Most of the data from spotted hyaenas were obtained from direct observations of hyaenas foraging, or from tracking spoor, between 1979 and 1982 (Mills *in prep.*).

At each carcass the species was recorded and at most a rough estimate of its age was made: if under about one year of age, or six months of age in the case of springbok, it was regarded as a juvenile; if over one year, or six months old in the case of springbok, but not fully grown according to horn length and shape, it was regarded as a sub-adult; and if it was judged to be full grown it was regarded as an adult. In addition to the above data the sex of the animal was noted and the bottom jaw collected whenever possible.

The predator was identified by examining the spoor around the carcass, looking particularly for signs of predator and prey running and for a struggle between the two. All carcasses up trees were assumed to be leopard kills and all carcasses on which cheetahs were observed feeding were assumed to have been killed by the cheetahs. In those cases (approximately half) where either of the above could be verified by spoor the assumption was proved to be correct. Lions and spotted hyaenas were only presumed to have been the killers of the carcass if this could be verified from spoor. Carcasses at which no killer could be identified were assumed to have died non-violently.

All bottom jaws collected from adult springbok, wildebeest and gemsbok were examined and then placed into one of five (springbok) or six (wildebeest and gemsbok) age-classes, according to the state of wear of the teeth (M. Mills *pers. comm.*), using similar methods to those of Kruuk (1972), Schaller (1972), Attwell (1980) and R. Liversidge (*pers. comm.*).

The main source of bias in the methods used for collecting much of the data, *i.e.* fortuitous observations, is that small prey animals are likely to be overlooked as they are eaten far more quickly and completely by the predators than are larger prey animals. This is further discussed at the relevant places in the text.

Results

Lions

Table 1 records those animals found to be killed by lions. Of the kills 221 (59,7%) were found along the riverbeds and 149 (40,3%) were found in the dunes. Nearly all the wildebeest (95,6%) were killed along the riverbeds and most of the gemsbok (74,2%) were killed in the dunes. In addition to the animals recorded in Table 1 lions were observed scavenging from 11 wildebeest, three eland, two springbok, one hartebeest and one gemsbok carcasses; 4,6% of all carcasses found on which lions had fed. Wildebeest and gemsbok are clearly the dominant food of lions, contributing 69,2% of all carcasses they fed on, the vast majority of which were kills.

Table 1

An analysis of lion kills from the southern Kalahari

Species	Number of carcasses				
	Adult	Subadult	Juvenile	Total	Percentage
Blue wildebeest	106	12	19	137	37,0
Gemsbok	78	10	32	120	32,4
Springbok	35	2	11	48	13,0
Red hartebeest	23	2	1	26	7,0
Eland	14	1	1	16	4,3
Ostrich	14	1	0	15	4,1
Porcupine	7	0	0	7	1,9
Aardvark	1	0	0	1	0,3
Total	278	28	64	370	

The proportions in which gemsbok are represented in the three age-classes in Table 1 do not differ significantly from the proportions in which they were found to be killed during 91 nights of tracking spoor by Eloff (1973a), when no kills could have been missed (chi-square = 1,78; df = 2; $P > 0{,}05$). This suggests that the gemsbok kill data presented in the present study closely represent the true proportions in which lions kill different aged gemsbok. Thus the possible bias in overlooking smaller, *i.e.* younger animals, mentioned earlier, does not appear to be a problem here. It also seems reasonable to assume that the data from the other large herbivores presented in Table 1 also reflect the true proportions that the three age-classes are taken by lions.

Adult animals form the bulk of lion kills, making up 75,1% of all kills. Species from which juveniles are relatively most commonly killed are gemsbok (26,7% of gemsbok kills) and springbok (22,9% of springbok kills).

Of 89 adult wildebeest killed by lions the sex ratio was 1 male per 1,4 females. The sex ratio of a sample of 7 391 live adult wildebeest sexed in the field between 1978 and 1982 was 1 male per 1,9 females (Binomial $P < 0{,}0003$; two-tailed). Taking this significant preponderance of females in the wildebeest population into account, the sex ratio of adult wildebeest killed by lions does not differ significantly from what would be expected if they were selecting equally from both sexes (chi-square = 2,18; df = 1; $P > 0{,}05$). By way of comparison the sex ratio of 103 adult wildebeest that died non-violently during the study period was 1 male per 0,8 females, a highly significant bias towards bull mortality (chi-square = 21,76; df = 1; $P < 0{,}001$).

Figure 1 shows the ratio of the percentages of 88 adult wildebeest of various age-classes killed by lions to the percentages of wildebeest of these age-classes from a sample of 31 randomly shot wildebeest, which are believed to represent the age structure of the living population. A clear trend towards higher predation rates in the older age-classes is apparent and the proportions in which animals in age-classes 1–3 and 4–6 are represented in the two samples are significantly different (chi-square = 7,01; df = 1; $P < 0{,}01$).

Fig. 1. The ratio of the percentages of adult wildebeest of each age-class killed by lions (n = 88) to the percentages of wildebeest of each age-class randomly shot (n = 31) and the ratio of the percentages of adult wildebeest of each age-class which died non-violently (n = 96) to the percentages of each age-class in the shot sample.

In addition, Fig. 1 shows the ratio of the percentages of 96 adult wildebeest of various age-classes which died non-violently to the percentages which were shot. A similar trend to that of lion caused mortality is seen, although there is not quite a statistical difference in the proportions in which animals in age-classes 1–3 and 4–6 are represented in the shot and non-violent mortality data (chi-square = 3,04; df = 1; $P > 0,05$).

During the period 1973–1977, 70 wildebeest carcasses killed by lions were found and five which died non-violently were found. During the period 1978–1982, 67 lion-killed wildebeest carcasses were found and 109 non-violent wildebeest mortalities were found, a highly significant difference (chi-square = 62,77; df = 1; $P < 0,001$).

Of 72 adult gemsbok killed by lions the sex ratio was 1 male per 0,6 females. The sex ratio of a sample of 494 live adult gemsbok sexed in the field between 1976 and 1982 was 1 male per 0,8 females (Binomial $P = 0,4654$; two-tailed). Lions, therefore, appear to select male gemsbok and significantly more bulls were found killed by lions than would be expected given the observed sex ratio in the living population (chi-square = 4,63; df = 1; $P < 0,05$). The sex ratio of 27 gemsbok which died non-violently was 1 male per 0,7 females which almost differs significantly from the expected ratio (chi-square = 3,75; df = 1; $P > 0,05$).

Figure 2 shows the ratio of the percentages of a sample of 45 gemsbok of various age-classes killed by lions to the percentages of gemsbok of these age-classes from a sample of 18 randomly shot gemsbok which, like the wildebeest, are assumed to represent the age structure of the living population. A slight tendency towards higher predation rates in older animals is apparent, although no significant difference in the proportions in which gemsbok in age-classes 1–3 and 4–6 are represented in the shot and lion-killed samples occurs (chi-square = 1,26; df = 1; $P > 0,05$). This may be because of the small sample size.

Fig. 2. The ratio of the percentages of adult gemsbok of each age-class killed by lions (n = 45) to the percentages of gemsbok of each age-class randomly shot (n = 18) and the ratio of the percentages of adult gemsbok of each age-class which died non-violently (n = 24) to the percentages of each age-class in the shot sample.

Figure 2 also shows the ratio of the percentages of 24 adult gemsbok of various age-classes which died non-violently to the percentages which were shot. The trend is very similar to that of lion predation, although the sample sizes are too small for statistical analysis. Non-violent mortality accounted for 15,7% of the known causes of gemsbok mortality during the study. There was, therefore, no evidence of a heavy non-violent mortality in gemsbok, as was found in the case of wildebeest.

In proportion to their numbers (Mills & Retief 1984) springbok do not appear to be a sought after prey species for lions, and accounted for only 13,0% of their kills (Table 1). Because of their small size, however, there may have been a tendency to overlook lions feeding on springbok, especially lambs, which they can consume in less than 5 minutes (*pers. obs.*). Adult springbok were killed by lions in the ratio of 1 male per 0,6 females. The sex ratio of a sample of 18 913 live springbok counted throughout the study was 1 male per 1,5 females (Binomial $P < 0,00001$; two-tailed). Lions therefore show a significant selection for springbok rams (chi-square = 5,18; df = 1; $P < 0,05$). The sample of bottom jaws from lion-killed springbok adults was too small for analysis of age selection.

Hartebeest are rarely caught by lions and constituted only 7,0% of lion kills. The sex ratio of 19 adult hartebeest killed by lions was 1 male per 0,3 females and the sex ratio of 490 adults in the living population between 1978 and 1982 was 1 male per 1,9 females (Binomial $P < 0,00001$; two-tailed). There was, therefore, a strong selection by lions for adult male hartebeest over adult females (chi-square = 16,8; df = 1; $P < 0,00001$).

Of the 14 adult eland found to be killed by lions eight were males and six were females and all age-classes were represented. Of the 14 ostriches found to be killed by lions seven were males and seven females.

The relatively high incidence of porcupines in the sample of lion kills, in spite of the built in bias against these small food items with the technique used, is worth noting. The phenomenon of Kalahari lions killing this and other types of small prey has been described and discussed in detail by Eloff (1973a, 1973b).

Spotted hyaenas

Table 2 shows the animals found to be killed by spotted hyaenas. These data were mainly collected from direct observations or tracking spoor and can confidently be taken to unbiasedly represent the type of prey taken by spotted hyaenas in the southern Kalahari. In addition to these prey items spotted hyaenas were observed to scavenge from the following carcasses: 17 wildebeest, 10 gemsbok, nine springbok, seven hartebeest, three eland and three steenbok *i.e.* 36,3% of the carcasses they were observed feeding on. In addition they eat numerous pieces of bone which they find scattered around their territories (Mills 1984).

Wildebeest and gemsbok contributed 63,0% of all carcasses fed on by spotted hyaenas and 67,5% of their kills. Juveniles formed the bulk of spotted hyaena kills (58,1%) with gemsbok calves alone making up 29,1% of all spotted hyaena kills. Wildebeest (six bulls and five cows) were the most commonly killed adult animals, but the small number of observations on adult prey species precludes any further sex or age selection analyses.

Table 2

An analysis of spotted hyaena kills from the southern Kalahari

Species	Number of carcasses				
	Adult	Subadult	Juvenile	Total	Percentage
Gemsbok	5	3	25	33	38,4
Blue wildebeest	11	3	11	25	29,1
Springbok	1	1	8	10	11,6
Eland	2	0	3	5	5,8
Ostrich	2	1	2	5	5,8
Red hartebeest	2	1	0	3	3,5
Porcupine	3	0	0	3	3,5
Steenbok	0	0	1	1	1,2
Springhare	1	0	0	1	1,2
Total	27	9	50	86	

Cheetahs

Table 3 lists the observed cheetah kills. It has been shown from tracking spoor by Labuschagne (1979) that small animals such as steenbok, springhares and hares, are important prey items for cheetahs, particularly when cheetahs are foraging alone and in the dunes. There is a significant difference in the proportions with which small animals (springhare, hare, steenbok, springbok lamb and bat-eared fox) versus animals larger than these occur in the samples of cheetah kills from Labuschagne's data and those presented here (chi-square = 12,57; df = 1; $P <$ 0,001). Furthermore, with the exception of one ostrich, one gemsbok calf and one steenbok kill, all my observations were made along the riverbeds. There is, therefore, a certain amount of bias in the cheetah kill data presented here.

Nevertheless springbok are clearly the most important prey species for cheetah in the Kalahari Gemsbok National Park, if not in the southern Kalahari as a whole, and made up 86,9% of their kills in the present study and 41% of the 59 kills in Labuschagne's (1979) study.

Because of their size springbok lambs, particularly those under one month of age, are no doubt under-represented in the present sample. Nevertheless they comprised 20,6% of all springbok killed by cheetahs, and are important prey for cheetahs. Of these lambs 81% were under three months of age, the majority being less than one month of age.

An indication of the rate at which cheetahs can kill small springbok lambs can be gleaned from observations of three subadults which killed four lambs of under one month old in a 60 hour period (R. Goss *pers. comm.*). Although not strictly seasonal breeders, springbok do synchronise their lambs to a marked degree, both temporally and spatially, and thus large numbers of small lambs are usually only available to predators for about two months per year (*pers. obs.*).

Table 3

An analysis of cheetah kills from the southern Kalahari

Species	Number of carcasses	Percentage
Springbok	199	86,9
Adult male	84	
Adult female	47	
Adult of unknown sex	25	
Subadult	2	
Lamb	41	
Ostrich	8	13,1
Wildebeest calf	8	
Gemsbok	6	
Subadult	2	
Calf	4	
Hartebeest calf	4	
Steenbok	2	
Bat-eared fox	2	
Total	229	

Of 131 adult springbok killed by cheetahs the sex ratio was 1 male per 0,6 females. Taking into account the preponderance of females in the living population referred to earlier (1 male per 1,5 females) cheetahs show a marked selection for males (chi-square = 32,65; df = 1; $P < 0,001$).

Figure 3 shows the ratio of the percentages of 82 adult springbok of known age killed by cheetahs to the percentages of springbok in these age-classes from a sample of 191 randomly shot animals. The data clearly show that springbok from the older adult age-classes (3, 4 and 5) are significantly more prone to cheetah predation than are younger adults (chi-square = 19,36; df = 4; $P < 0,001$).

The two subadult gemsbok killed by cheetahs (Table 3) were done so by two males in the space of one week. One further observation of these two animals killing a large gemsbok has recently been recorded (R. Goss *pers. comm.*). It seems, therefore, that these two individuals had developed a technique for overcoming larger prey than is normal for cheetahs. Such individual specialisations in hunting techniques have been recorded in other carnivores (Kruuk 1976; Mills 1978).

Leopards

Table 4 lists the observed leopard kills divided up into those found along the riverbeds and those found in the dunes. Springbok comprised 81% of all kills found along the riverbeds, but in the dunes particularly, leopards are far more catholic in their diet. A comparison of my data collected in the dunes with those of Bothma & Le Riche (*in press*) collected from tracking spoor in the dunes revealed no statisti-

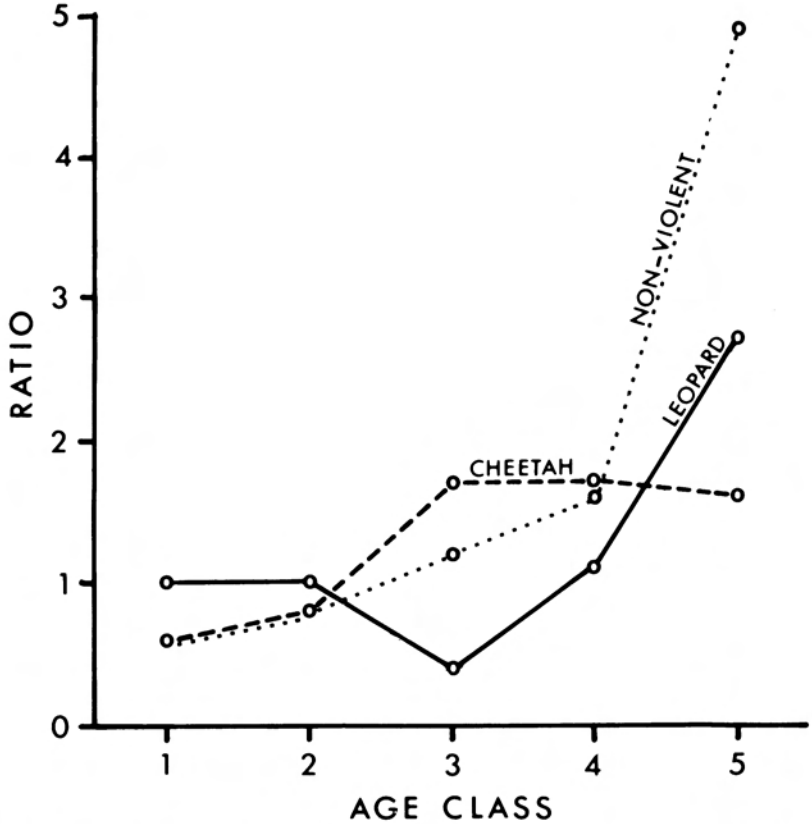

Fig. 3. The ratio of the percentages of adult springbok of each age-class killed by cheetahs (n = 82) to the percentages of springbok of each age-class randomly shot (n = 191), the ratio of the percentages of adult springbok of each age-class killed by leopards (n = 18) to the percentages of each age-class in the shot sample, and the ratio of the percentages of adult springbok of each age-class which died non-violently (n = 29) to the percentages of each age-class in the shot sample.

cal difference in the frequencies with which relatively large animals (aardvark *Orycteropus afer*, duiker, ostrich, porcupine, springbok adults and eland, gemsbok and hartebeest juveniles) and small animals (the rest) occurred in the diets of leopards in the two studies (chi-square = 0,03; df = 1; $P > 0,05$). Again this adds credence to the data presented here.

Of the adult springbok killed by leopards the sex ratio was 1 male per 0,6 females. Like lions and cheetahs, therefore, leopards show a significant selection for male springbok (chi-square = 5,22; df = 1; $P < 0,05$). Of 18 adult springbok killed by leopards that were aged (Fig. 3), the heaviest mortality was in the oldest age-class. There was, however, no significant difference in the proportions with which young adult springbok (age-classes 1 and 2) as opposed to older animals (age-classes 3 to 6) were represented in the leopard kills and shot samples (chi-square = 0,19; df = 1; $P > 0,05$), but this may be due to the small size of the sample.

Table 4

An analysis of leopard kills from the southern Kalahari.

Species	Number of carcasses			
	River	Dunes	Total	Percentage
Springbok	48	4	52	65,0
Adult male	16	0	16	
Adult female	10	0	10	
Adult of unknown sex	8	1	9	
Subadult	4	1	5	
Lamb	10	2	12	
Hartebeest calf	2	3	5	35,0
Steenbok	0	5	5	
Black-backed jackal	2	1	3	
Gemsbok calf	0	2	2	
Ostrich	1	1	2	
Duiker	0	2	2	
Wildebeest calf	1	0	1	
Bat-eared fox	1	0	1	
Cape fox	1	0	1	
Aardwolf	0	1	1	
Wild cat	0	1	1	
Ground squirrel	1	0	1	
Cheetah	1	0	1	
Aardvark	0	1	1	
Mice	1	0	1	
Total	59	21	80	

In comparing the samples of springbok killed by cheetahs and leopards (Tables 3 and 4), there is a significant difference in the proportions in which adult males, adult females, subadults and lambs appeared in the two samples (chi-square = 12,93; df = 3; $P < 0{,}01$). This is particularly so with subadults, which were far better represented in the leopard sample than the cheetah one.

Non-violent mortality accounted for only 13,2% of all springbok mortality. The sex ratio of 32 adult springbok which died non-violently was 1 male per 1,1 females, which does not differ significantly from the expected ratio (chi-square = 0,69; df = 1; $P > 0{,}05$). Figure 3 shows the ratios of the percentages of 29 adult springbok of each age-class which died non-violently to the percentages of each age-class in the population and shows a progressive increase in non-violent mortality with age. In spite of the small sample size, there was a significant difference in the proportions with which old (age-classes 3, 4 and 5) as opposed to young (age-classes 1 and 2) adults were represented in the non-violent mortality and shot samples (chi-square = 6,72; df = 1; $P < 0{,}01$).

Discussion

Ecological separation of the predators

The four dominant large predators in the southern Kalahari can be divided into two groups for the purpose of a discussion on ecological separation. There are the two predominantly large to medium-sized mammal predators; lions and spotted hyaenas, and the two predominantly medium-sized to small mammal predators, leopards and cheetahs.

Lions and spotted hyaenas are both mainly nocturnal, use the same habitats more or less equally (*pers. obs.*) and feed mainly on wildebeest and gemsbok (Tables 1 and 2). There is, therefore, a great deal of overlap in the ecological interests of these two species and consequently a high degree of aggression is shown towards each other when they meet up, even when no food is present (Kruuk 1972; *pers. obs.*).

The extent to which their diets overlap in the southern Kalahari, however, is lessened by differences in selection of their two most common prey species. Lions kill mainly adults and subadults of both species, whereas spotted hyaenas kill mainly calves. This is particularly marked in the case of gemsbok calves which make up 29,1% of spotted hyaena kills and only 8,6% of lion kills. Additionally spotted hyaenas are far better adapted to scavenging than lions are and a substantial amount of their food is scavenged. When scavenging from large and medium-sized mammals spotted hyaenas are in direct competition with brown hyaenas (Mills & Mills 1982; Mills 1984).

Similarly, there are several mechanisms which tend to reduce the amount of competition between leopards and cheetahs. Although along the riverbeds they both feed predominantly on springbok, the proportions in which they select from different age segments of the springbok population may differ slightly, as leopards appear to take more subadults than cheetahs (Tables 3 and 4). Furthermore, cheetahs are almost exclusively diurnal hunters and leopards are almost exclusively nocturnal, which also tends to reduce the amount of exploitation competition. Finally, leopards appear to have a much wider diet than cheetahs do (Labuschagne 1979; Bothma & Le Riche 1984; this study).

The effect of predation on the prey population

What effect do the predators have on their prey populations in the southern Kalahari? This extremely important ecological question is difficult to answer fully, although there is now enough information available from the southern Kalahari to begin to do so.

The ungulate populations in the southern Kalahari are largely nomadic, and, therefore, extremely difficult to quantify. At certain times there are thousands of animals in an area, at others very few (Bothma & Mills 1978; Mills & Retief 1984; *pers. obs.*). The predators on the other hand are in the main restricted to territories, albeit large ones, and there are no indications that they follow the movements of their prey to any extent (Eloff 1973a, 1973b; Mills *in prep.*; *pers. obs.*). The lion population of the Kalahari Gemsbok National Park is approximately 140 (Mills, Wolff, Le Riche & Meyer 1978) and the spotted hyaena population approximately

85 (Mills 1984). The numbers of leopards and cheetahs are unknown, but it is believed that there are not more than 100 leopards and 60 cheetahs in the Kalahari Gemsbok National Park (*pers. obs.*). The numbers of all these predators are, no doubt, mainly limited by the nomadic nature of their prey and their own sedentary behaviour, which results in there being periods of very low food availability in each territory or home range.

Wildebeest are important prey species for both lions and spotted hyaenas (Tables 1 and 2). Lions are the most important predators of the adults and they tend to remove mainly older animals (Fig. 1). The significant increase in non-violent mortality of wildebeest after 1977, which was the end of a high rainfall period, coupled with the apparent drop in wildebeest numbers over the succeeding years (Mills & Retief 1984), strongly suggests that predators are of little consequence in regulating wildebeest numbers. Furthermore the distorted sex ratio of adult wildebeest seems to be a consequence of a high non-violent mortality in bulls, and not due to differential predation on bulls and cows by lions. Although wildebeest calves are taken by both lions and spotted hyaenas, and also occasionally by leopards and cheetahs, there is no suggestion, even in relative terms, of a heavy predation on wildebeest calves during the calving season as, for example, has been found to be exerted by spotted hyaenas in the Ngorongoro Crater (Kruuk 1972).

With gemsbok the situation is more difficult to judge. Gemsbok tend to be more sedentary than the other ungulates and no high incidences of non-violent mortality amongst the gemsbok were noticed during the study. Predation on gemsbok calves is comparatively higher than on wildebeest calves, particularly by spotted hyaenas (Tables 1 and 2). Furthermore, gemsbok are far less seasonal breeders than the other ungulates are (*pers. obs.*), so that predation on calves is more evenly spread throughout the year, thus potentially making the impact of predation heavier than on a more synchronised breeder.

However, spotted hyaena numbers are comparatively low and judging by the long distances, up to 70 km, that they sometimes have to travel in their search for food (Mills *in prep.*), it is doubtful that they have a major influence on the gemsbok population. Adult gemsbok predation which is mainly by lions (Table 1) tends to mirror that of non-violent mortality (Fig. 2), suggesting that lions are mainly removing surplus animals.

Cheetahs prey heavily on young springbok lambs, which also have a wide range of other predators, from lions to martial eagles *Polemaetus bellicosus* (*pers. obs.*). Whilst in the riverbeds, and particularly the Auob riverbed, which has the highest density of cheetahs in the southern Kalahari (*pers. obs.*), predation on springbok lambs may be relatively heavy. However, once past the critical first few weeks of life, the lambs become far more difficult to catch. Although non-violent mortality did not appear to be heavy on springbok during the study, cheetahs and leopards (Fig. 3), and to a lesser extent lions, mainly catch older adult animals, particularly males, which are the most expendable segment of the population. Once again, therefore, it would seem that the predators remove predominantly surplus animals from the springbok population and do not exert a great influence on the population. Predation does, however, seem to influence the structure of the springbok population and may be responsible for the distorted sex ratio of adult springbok.

The incidence of eland, hartebeest and ostriches in the diets of the carnivores is so low that there is no question of predation having any great impact on their populations.

Although predation appears in general to have a small impact on prey numbers in the southern Kalahari, as it does in other large, natural areas (Schaller 1972), predation may, on an evolutionary time-scale, have had a considerable influence on the form and behaviour of many of the ungulates (Bertram 1979). The alertness of the hartebeest, the agility of the springbok, the stamina of the wildebeest and the rapier-like horns of the gemsbok, to quote but one example from each, all help individual animals to escape predation. Those that are not as well endowed with these characteristics as others are more likely to be caught and, therefore, less likely to perpetuate their genes.

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