CHAPTER 5

INTERRELATIONSHIPS BETWEEN THE LARGER CARNIVORES

As with the leopard, little data have been published on the interrelationships between the larger African carnivores - the lion, the leopard, the cheetah, the spotted hyaena and the wild dog. Most research on the larger African carnivores has been directed towards the ecology and behaviour of single species with brief mentions of interrelationships (e.g. Pienaar 1969, Schaller 1972, Eloff 1973 and Bothma and Le Riche 1984).

When predators hunt in the same area, then competition for limited food is likely of occur (Schaller 1972) and that competition between individuals of different species has an influence on the niches of the species (Eaton 1979) and the distribution of the species (Schaller 1972). The hypothesis of Eaton (1979) is that direct competition may favour grouping and that the grouping of individuals in a species influences the ability to win in direct competition with individuals of other species. In the interspecific rank of larger African predators, Eaton (1979) rates lion groups above groups of spotted hyaenas and groups of wild dogs. Following the spotted hyaena and wild dog groups is a single male lion followed by a single lioness. The solitary

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leopard is ranked fifth followed by a single spotted hyaena. A single brown hyaena, a single cheetah and a single wild dog are ranked below a single spotted hyaena in this order. A group of cheetahs possibly ranks equal to a single leopard and a single spotted hyaena. Ranked above all is man (Eaton 1979). Scott (1985) suggested that weight and body size correlated with the ability of predators to win encounters over food.

Although competition does occur and that in general, predators are intolerant of each other, and view each other as competitors, competition is reduced by ecological separation and different behavioural patterns of the various predators e.g. habitat selection, prey selection and activity times (Schaller 1972). However, the different predators are not completely separated in time and space and clashes, sometimes fatal, are inevitable (Schaller 1972).

Bertram (1982) has shown that lions and leopards can co-exist in the same habitat - the range of an adult female leopard and her full-grown female cub fell within the range of a pride of four lionesses. In Bertram's (1982) study, prey availability for both the lions and the leopards were the same and that competition was reduced by the two different predators preying on different prey types. The leopard's tree climbing ability was another factor allowing the lion and the leopard to co-exist (Bertram 1982).

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Seidensticker (1976) postulated that three factors enabled the lion and the leopard to co-exist in the Royal Chitawan National Park: a large prey biomass, a large proportion of this biomass being of the smaller size classes and the dense vegetation structure.

A knowledge of the interrelationships between carnivores, both inter - and intraspecific, is important for their successful management and conservation (Mills 1984 and Hornocker and Bailey 1986), and also leads to an understanding of the evolution of social systems among carnivores (Mills 1984). As an example, Mills (1984) has postulated, from a relationship study, that an increase in ungulate numbers would favour an increase in spotted hyaena numbers and a subsequent decrease in brown hyaena numbers in the southern Kalahari. Altering one factor in a system could therefore lead to a chain reaction, either adversely affecting or favouring carnivore populations occurring together in one area.

The aim of this part of the study was to gain an insight into the interrelationships between the larger carnivores of the Klaserie Private Nature Reserve. The information gained could then hopefully be used in the successful management and conservation of larger Klaserie carnivores.

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MATERIALS AND METHODS

Data on interrelationships between the five main carnivores were based on activity patterns, either directly or indirectly via sightings, tracks and vocalizations and on kills located in the field. Data on interrelationships were collected throughout the reserve. Special reference is made to the leopard and the cheetah.

Prey types and availability can be described as largely uniform throughout the reserve, except along the Klaserie and Ntsiri Rivers where bushbuck, waterbuck and other riverine favouring animals occur. There are no seasonal herbivore migrations in the Klaserie Private Nature Reserve.

RESULTS AND DISCUSSION

Leopard And Lion

The lion is the leopards closest competitor and also the leopard's closest relative (Bertram 1982).

No actual contact between lions and leopards was witnessed during the study period.

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In the study area, tracks of lions were less frequently encountered than those of leopards and lion tracks were followed for longer distances. It is concluded that lion prides in the Klaserie Private Nature Reserve had larger ranges than leopards and that the ranges of leopards fell within different pride ranges. Viljoen (**pers. comm.**) indicated larger home ranges for Klaserie lions than leopards and that the Klaserie Private Nature Reserve or parts thereof were occupied by different lion prides.

On 10 occasions tracks showed that lions and leopards had used the same section of road on the same night but at different times. In some instances the lion/s had moved before the leopard/s and in the other instances, the leopard/s before the lion/s. On a further four occasions when lions and leopards were known to have moved around in the same area on the same night, their tracks were 300 m, 900 m, 1100 m and 1400 m apart. For the remainder of the study the tracks of lions and leopards were found on separate nights. Figure 11 shows that lions and leopards were active predominantly during the hours of darkness with an overlap of activity times.

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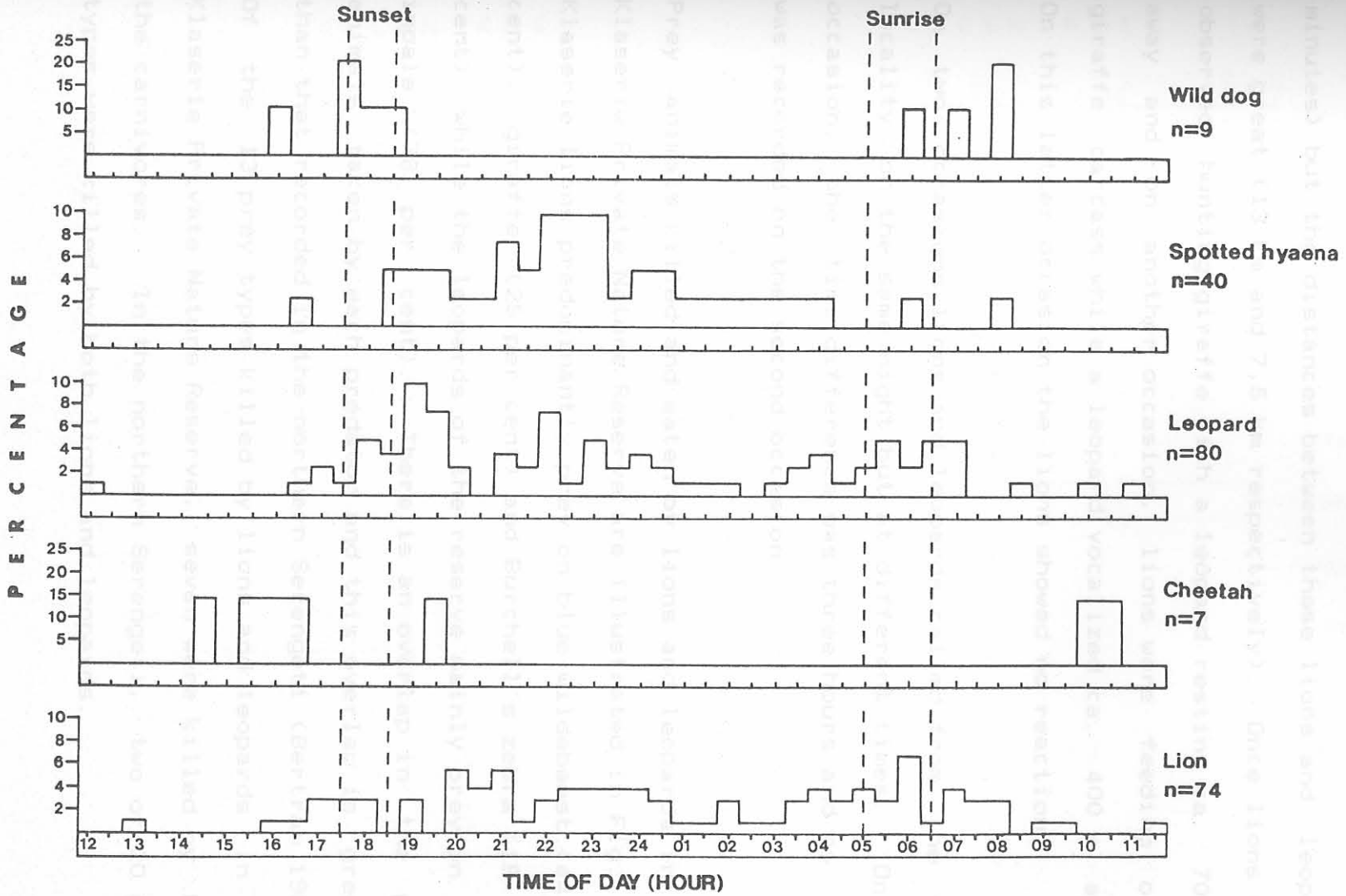

Figure 11: Periods of activity (percentage of observations) of different types of larger carnivores in the Klaserie Private Nature Reserve, Eastern Transvaal Lowveld, February 1979 to October 1981.

On two occasions active lions and leopards were sighted within a relatively short space of time (35 minutes and 20 minutes) but the distances between these lions and leopards were great (13 km and 7,5 km respectively). Once lions were observed hunting giraffe with a leopard resting ca. 700 m away and on another occasion, lions were feeding on a giraffe carcass while a leopard vocalized ca. 400 m away. On this latter occasion the lions showed no reaction.

On two occasions lions and leopards called from the same locality on the same night but at different times. On one occasion, the time difference was three hours and no time was recorded on the second occasion.

Prey animals killed and eaten by lions and leopards in the Klaserie Private Nature Reserve are illustrated in Fig. 12. Klaserie lions predominantly prey on blue wildebeest (44 per cent), giraffe (25 per cent) and Burchell's zebra (15 per cent) while the leopards of the reserve mainly prey on the impala (78 per cent). There is an overlap in the prey animals taken by each predator and this overlap is greater than that recorded in the northern Serengeti (Bertram 1982). Of the 13 prey types killed by lions and leopards in the Klaserie Private Nature Reserve, seven were killed by both the carnivores. In the northern Serengeti, two of 20 prey types were killed by both lions and leopards.

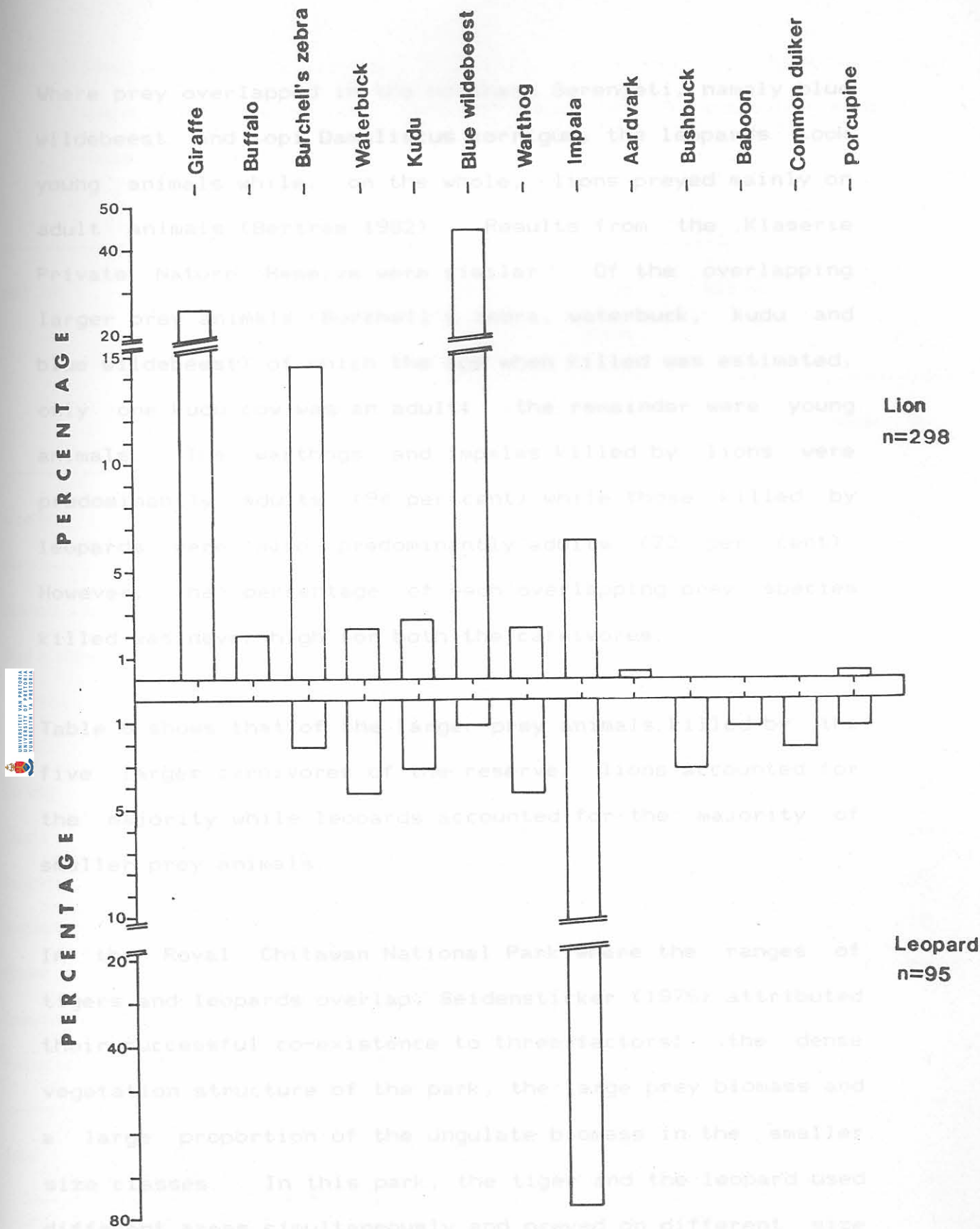

Figure 12: The percentage occurrence of different prey types in the diet of lions and leopards in the Klaserie Private Nature Reserve, Eastern Transvaal Lowveld, February 1979 to October 1981.

Where prey overlapped in the northern Serengeti, namely blue wildebeest and topi **Damaliscus korrigum**, the leopards took young animals while, on the whole, lions preyed mainly on adult animals (Bertram 1982). Results from the Klaserie Private Nature Reserve were similar. Of the overlapping larger prey animals (Burchell's zebra, waterbuck, kudu and blue wildebeest) of which the age when killed was estimated, only one kudu cow was an adult; the remainder were young animals. The warthogs and impalas killed by lions were predominantly adults (94 per cent) while those killed by leopards were also predominantly adults (72 per cent). However, the percentage of each overlapping prey species killed was never high for both the carnivores.

Table 6 shows that of the larger prey animals killed by the five larger carnivores of the reserve, lions accounted for the majority while leopards accounted for the majority of smaller prey animals.

In the Royal Chitawan National Park where the ranges of tigers and leopards overlap, Seidensticker (1976) attributed their successful co-existence to three factors: the dense vegetation structure of the park, the large prey biomass and a large proportion of the ungulate biomass in the smaller size classes. In this park, the tiger and the leopard used different areas simultaneously and preyed on different size classes of prey: the leopard in the 25 - 50 kg range and the

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Table 6: Overall percentage of each prey type killed by the five larger carnivores of the Klaserie Private Nature Reserve, Eastern Transvaal Lowveld, February 1979 to October 1981. Prey animals killed include all age classes.

PREY TYPE	LION		LEOPARD		CHEETAH		SPOTTED HYAENA		WILD DOG		TOTAL	
	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%
Giraffe	75	97,4	-	-	-	-	2	2,6	-	-	77	100
Buffalo	6	100,0	-	-	-	-	-	-	-	-	6	100
Burchell's zebra	43	95,6	2	4,4	-	-	-	-	-	-	45	100
Blue wildebeest	131	98,5	1	0,75	1	0,75	-	-	-	-	133	100
Waterbuck	7	63,6	4	36,4	-	-	-	-	-	-	11	100
Kudu	8	61,5	3	23,1	1	7,7	1	7,7	-	-	13	100
Warthog	7	58,4	4	33,3	1	8,3	-	-	-	-	12	100
Impala	19	14,7	74	57,4	23	17,8	6	4,7	7	5,4	129	100
Aardvark	1	100,0	-	-	-	-	-	-	-	-	1	100
Bushbuck	-	-	3	75,0	-	-	-	-	1	25,0	4	100
Baboon	-	-	1	100,0	-	-	-	-	-	-	1	100
Common duiker	-	-	2	66,7	1	33,3	-	-	-	-	3	100
Porcupine	1	50,0	1	50,0	-	-	-	-	-	-	2	100
Total	298		95		27		9		8		437	

- = No data

tiger in the 50 - 100 kg range. Similarly, Klaserie leopards also prey on a smaller size class of prey than the lions in the area and so did leopards in the northern Serengeti (Bertram 1982).

Unlike Klaserie leopards, leopards in the Royal Chitawan National Park rarely used roads but tigers did so frequently. Bertram (1982) observed that lions chased leopards whenever they saw them and concluded that the "presence of trees or rocks as retreats is presumably what makes it possible for leopards to co-exist with their larger rivals." Seidensticker (1976) only found leopards in trees when they had kills in trees and as in the present study, observed no "overt interactions" besides the possibility of a tiger having robbed a leopard of its kill. Schaller (1972) concluded that a riverine forest may not be the preferred habitat of a leopard but rather a refuge from lions. Although behavioural patterns may vary from area to area, the rock and tree escape means is not considered an important co-existence factor in the Klaserie Private Nature Reserve. The Klaserie Private Nature Reserve does not have the varied habitats that the Serengeti has and both the riverine and the woodland vegetation of the reserve are utilized successfully and simultaneously by both the lion and the leopard.

In the Royal Chitawan National Park, the chances of a tiger

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and a leopard meeting were reduced by the leopard using areas not frequented by the tiger, by differences in habitat preference and by the difference in activity patterns. Seidensticker (1976) further concluded that the leopard moved primarily independently of the tiger and that olfactory and visual senses came into play at close range when the leopard could detect and avoid the tiger. Social dominance was a central factor in tiger - leopard coactions. The data from the present study are too meagre to conclude whether the Klaserie leopard would use areas which were not frequented by lions and to conclude how the two predators avoided each other. Only continued simultaneous surveillance of a leopard and lion/s in an area would prove this. However, there is no evident habitat selection by lions and leopards in the Klaserie Private Nature Reserve.

In agreement with Seidensticker (1976) and Eltringham (1979) one important factor in the successful co-existence of Klaserie lions and Klaserie leopards is the availability of prey of suitable size classes for both predators.

Research so far has indicated that the lion and the tiger are both socially dominant over the solitary leopard (Schaller 1972, Seidensticker 1976, Bertram 1982 and Bothma and Le Riche 1984).

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Leopard And Cheetah

No direct contact between leopards and resident cheetahs was observed during the present study. As recorded, one released cheetah may have been killed by a leopard.

Cheetahs and leopards used the same woodland habitat of the Klaserie Private Nature Reserve. The ranges of leopards and cheetahs overlapped with indications that the range of the cheetah is larger than that of the leopard. Cheetah tracks were not frequently encountered and cheetahs were not as often seen as leopards or lions. The cheetah population in the Klaserie Private Nature Reserve was probably quite low, as is normal in other areas (Schaller 1972 and Hamilton 1981).

On four occasions, leopard and cheetah tracks were found on the same section of road in a 16 hour period; tracks were together for 15 m, 20 m, and 30 m and on the fourth occasion, the tracks simply crossed paths. On a fifth occasion, tracks were found in the same locality, 40 m apart. On other occasions, tracks were found separately on different days. On one occasion it was definitely established that a cheetah had moved along following a leopard.

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Although little data exist on cheetah movements in the Klaserie Private Nature Reserve, it is accepted that Klaserie cheetahs were predominantly diurnal, while Klaserie leopards were predominantly nocturnal (Fig. 11). On one occasion when cheetahs and leopards were seen in relative close proximity was when two subadult leopards were resting together on a rock and three adult cheetahs were resting 400 m away.

As recorded, the leopards of the Klaserie Private Nature Reserve preyed on 10 prey types, but predominantly so on the impala. The resident cheetahs of the reserve were known to prey on five prey types, also predominantly impalas. Prey animals killed and eaten by cheetahs and leopards are shown in Fig. 13. All prey animals killed by Klaserie cheetahs (kudu, blue wildebeest, warthog, impala and common duiker) were also killed by leopards in the reserve. Impala comprised 85 per cent (n = 23) of cheetah kills and 78 per cent (n = 74) of leopard kills. Of known age impalas killed by cheetahs, 47 per cent (n = 15) were adults. The remaining 53 per cent were subadult animals. Two female impalas killed were in the advanced stage of pregnancy with the unborn lambs being eaten as well. Of impalas killed by leopards, 75 per cent (n = 47) were adults. Most cheetah kills (78 per cent) in the Serengeti area were of prey in the 20 - 100 kg size class (Kruuk and Turner 1967) and in the Kafue National Park, Zambia, puku **Kobus vardonii**

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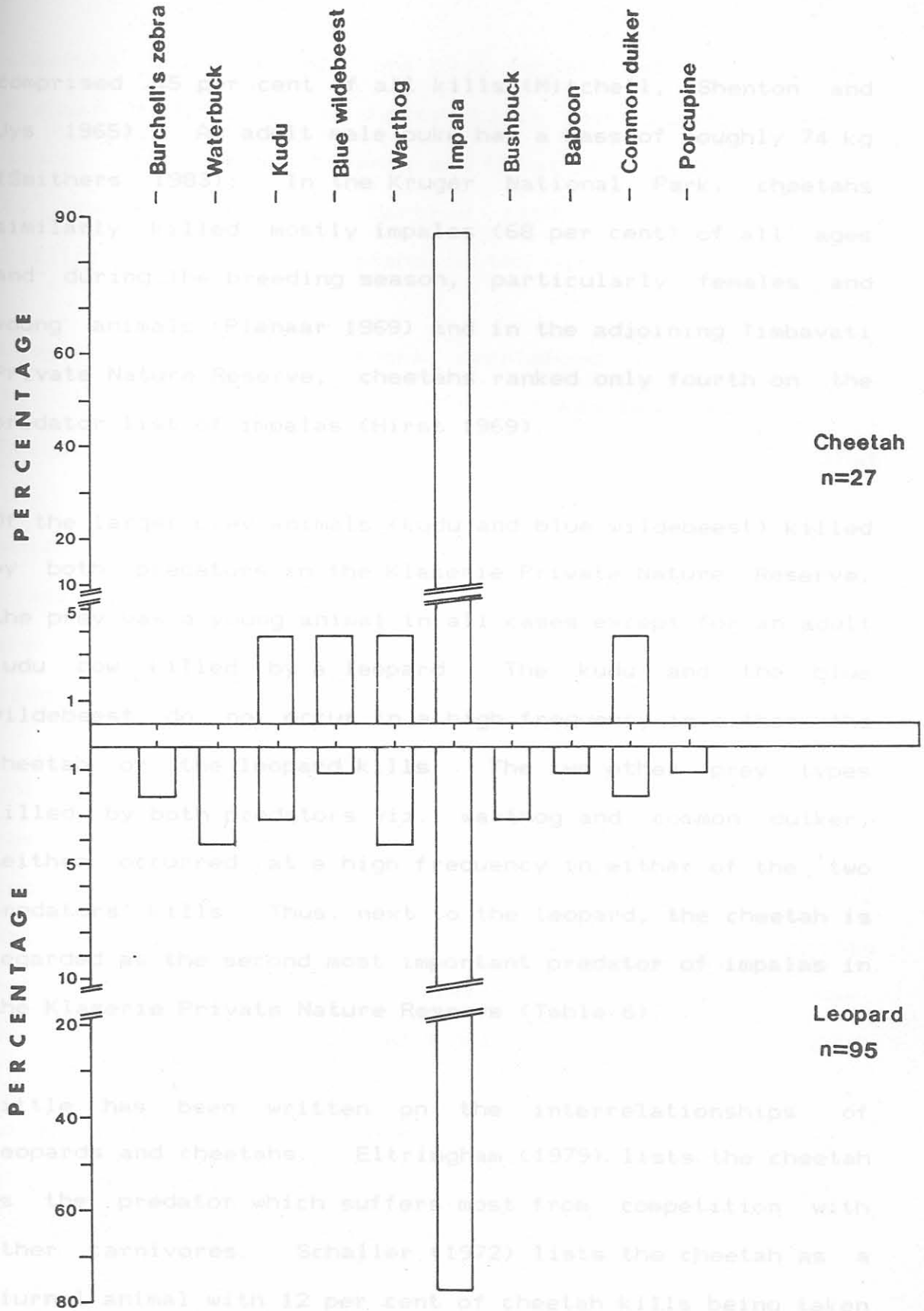

Figure 13: The percentage occurrence of different prey types in the diet of cheetahs and leopards in the Klaserie Private Nature Reserve, Eastern Transvaal Lowveld, February 1979 to October 1981.

comprised 45 per cent of all kills (Mitchell, Shenton and Uys 1965). An adult male puku has a mass of roughly 74 kg (Smithers 1983). In the Kruger National Park, cheetahs similarly killed mostly impalas (68 per cent) of all ages and during the breeding season, particularly females and young animals (Pienaar 1969) and in the adjoining Timbavati Private Nature Reserve, cheetahs ranked only fourth on the predator list of impalas (Hirst 1969).

Of the larger prey animals (kudu and blue wildebeest) killed by both predators in the Klaserie Private Nature Reserve, the prey was a young animal in all cases except for an adult kudu cow killed by a leopard. The kudu and the blue wildebeest do not occur in a high frequency in either the cheetah or the leopard kills. The two other prey types killed by both predators viz. warthog and common duiker, neither occurred at a high frequency in either of the two predators' kills. Thus, next to the leopard, the cheetah is regarded as the second most important predator of impalas in the Klaserie Private Nature Reserve (Table 6).

Little has been written on the interrelationships of leopards and cheetahs. Eltringham (1979) lists the cheetah as the predator which suffers most from competition with other carnivores. Schaller (1972) lists the cheetah as a diurnal animal with 12 per cent of cheetah kills being taken over by other predators in the Serengeti and two adult

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cheetahs being killed, one by a leopard and one by a lion. Pienaar (1969) records cheetah kills being appropriated by lions, leopards and hyaenas and cheetahs even being killed by these predators. Bertram (1982) reported leopards killing the young of cheetahs in the northern Serengeti.

Leopard and cheetah ranges overlapped in the Klaserie Private Nature Reserve and both utilised the same habitat. Accepting that leopards are dominant over cheetahs and that the cheetah is a weak competitor, three factors are evident which allow the cheetah and the leopard to co-exist in the Klaserie Private Nature Reserve: different activity times, the feeding behaviour of the cheetah and differences in range size.

Unlike Kalahari Desert cheetahs (Lubuschagne 1979), the cheetahs in the reserve are predominantly diurnal while the leopard is active mainly at night. In the Klaserie Private Nature Reserve, both predators prey predominantly on impalas but the leopard takes a wider range of prey types. Further, cheetahs in the reserve were not known to scavenge which could bring them into closer contact with leopards (and other carnivores). Only two areas are known to report cases of cheetahs scavenging, in the Kruger National Park (Pienaar 1969) and on the Serengeti Plains (Caro 1982).

Having made a kill in the Klaserie Private Nature, cheetahs

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rapidly fed on a carcass and then vacated the area with little remaining of the kill and without their presence really becoming known to a leopard. That cheetahs rapidly feed on a carcass has been found elsewhere (Schaller 1972 and Wrogemann 1975). Labuschagne (1979) reported cheetahs to be very nervous feeders, constantly looking around while feeding, on the alert for lions, leopards, spotted hyaenas and jackals all of which can drive cheetahs from their kills. Wrogemann (1975) suggested, and her views are supported here, that this type of behaviour reduces the chance of interactions between cheetahs and other carnivores.

If Klaserie cheetahs occupied the same range size as Klaserie leopards, then the chance of a contact would be greater. By presumably occupying larger ranges, the chance of a contact is lessened, although a larger cheetah range would increase the chance of contacts with different leopards.

Eaton (1979) ranks the cheetah below the leopard in the interspecific behavioural rank of the larger African predators and states that "leopards usually attack and win against cheetahs." In the Serengeti National Park (Schaller 1972), cheetahs and leopards are separated in space and time: cheetahs there inhabit the plains and the woodland/plains borders whereas the leopard inhabits

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riverine forests and thickets. Cheetahs there are diurnal and leopards nocturnal. Both animals preyed mainly on Thomson's gazelle with the leopard taking a wider range of prey types. In the Kalahari Desert (Labuschagne 1979) cheetahs and other larger carnivores are neither separated in time nor space and competition is reduced by the low densities of all carnivores there. Klaserie leopards and cheetahs are largely separated in time but not in space. Both prey on the same size class of prey with chance interactions being further reduced by the cheetah's feeding behaviour. The cheetah is the third most important predator in the Klaserie Private Nature Reserve and only a detailed study on them would reveal their true interrelationships with Klaserie leopards.

Leopard And Spotted Hyaena

Leopards were known to make contact with spotted hyaenas on two occasions in the Klaserie Private Nature Reserve.

On one night at 20h40 one spotted hyaena was feeding on the carcass of an adult kudu bull which had died a natural death. At 21h00 the spotted hyaena became restless (sniffing the air and looking around) and suddenly left the immediate area. It was suspected that lions were arriving at the carcass. Soon thereafter an adult female leopard arrived at the carcass and began feeding. After some 15

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minutes two spotted hyaenas (one larger than the other) suddenly rushed the leopard which ran away. The larger of the two hyaenas chased the leopard for a little distance. The two hyaenas resumed feeding. At 21h40 the leopard was sighted crouching 20 m from the carcass whereupon it charged the two hyaenas, swatting and growling. The two hyaenas fled and the leopard resumed feeding. Three hyaenas then arrived at the carcass and lay or sat close to the carcass. The larger hyaena twice crawled closer to the leopard, but every time it was swatted by the leopard. After 20 minutes of feeding, the leopard rose, rolled, cleaned herself and then moved away. The three hyaenas then resumed feeding with two black-backed jackals calling close by.

On another occasion an already fed on impala carcass was found under a marula tree at 22h15. Soon afterwards one spotted hyaena arrived at the carcass whereupon a smallish leopard appeared from the tree above. The leopard fed for 25 minutes with the one hyaena and one black-backed jackal circling the carcass. No attempt was made by the hyaena to take over the carcass and the leopard showed no interest in the hyaena. After feeding, the leopard moved away with the jackal following, yelping. The hyaena dragged the remains of the impala carcass away.

A report was also received of a single leopard chasing one spotted hyaena away from a carcass.

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Similar interactions have been reported from elsewhere. In the Kalahari Desert, Bothma and Le Riche (1984) observed that single male leopards defended their kills from two spotted hyaenas on two known occasions. Eaton (1979) states that single leopards always win against single spotted hyaenas but that a group of spotted hyaenas will dominate a single leopard. Two spotted hyaenas are usually enough to dominate a single leopard. That a single leopard dominates a single spotted hyaena is supported here but not that a group of spotted hyaenas will always win against a single leopard. A single leopard can dominate two or even three spotted hyaenas. Mills (In press) concluded that a single male leopard in the Kalahari Desert may dominate a small group of spotted hyaenas, particularly if the hyaenas are young. However, the incidences outlined by Mills (In press) indicate that even one spotted hyaena will dominate a single leopard in the Kalahari Desert. Henschel (1986) observed one spotted hyaena and one leopard to feed together for an hour on the same carcass in the Kruger National Park and that spotted hyaenas never avoided leopards and always approached them. On the other hand, leopards tended to avoid spotted hyaenas. Spotted hyaena group size was not important in interactions with leopards and that when spotted hyaenas showed aggressive behaviour towards a leopard, the spotted hyaenas dominated the leopard (Henschel 1986). In the Klaserie Private Nature Reserve, there was no evidence to suggest that leopards avoided spotted hyaenas

while the data suggest that spotted hyaenas in the Klaserie Nature Reserve do not avoid leopards.

In the Klaserie Private Nature Reserve, spotted hyaenas and leopards were both predominantly nocturnal (Fig. 11) but the spotted hyaena was not considered an important predator of those prey types utilized by leopards (Table 6). The spotted hyaenas in the reserve mainly appear to have a scavenging existence and are not as active predators as has been recorded elsewhere (Hirst 1969, Kruuk 1972 and Schaller 1972). Similarly, in the adjacent Timbavati Nature Reserve, spotted hyaenas were believed to scavenge much of their food or to hunt impalas which can be pulled down by one or two hyaenas (Bearder 1977, from Mills 1978). Mills (1978) argued that a woodland habitat, such as Timbavati, would hinder cursorial pack-hunting which is why spotted hyaenas were most often encountered singly or in pairs in such a habitat. In the Klaserie Private Nature Reserve, foraging spotted hyaenas were also most often encountered singly or in pairs and the tracks of spotted hyaenas in Klaserie also indicated this to be the case. As the Klaserie Private Nature Reserve is also a woodland habitat, the argument of Mills (1978) is supported. Most food items found in the faeces of spotted hyaenas in the Timbavati Private Nature Reserve were of very large (> 400 kg), large (80 - 400 kg), and medium-sized (12 - 80 kg) mammals (Bearder 1977, from Mills 1978). Of prey animal types known to have been killed

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by spotted hyaenas, two prey types were also killed by leopards (Fig. 14). Where age and sex was estimated at spotted hyaenas kills, three of the six impalas killed were adult females and one a subadult male. Two impala kills were neither aged nor sexed. The two giraffes killed by spotted hyaenas were both young animals and the kudu killed was an adult kudu female. The condition of the prey of the spotted hyaenas was not known nor was it known if they were in any way injured. Hirst (1969) lists the spotted hyaena as the third most important predator of impalas in the adjoining Timbavati Private Nature Reserve, below the leopard and the jackal.

The factor which is most likely to bring Klaserie leopards and Klaserie spotted hyaenas into closer contact is the habit of both animals to scavenge. Leopards will approach feeding spotted hyaenas, and spotted hyaenas will approach feeding leopards. Klaserie leopards did not frequently take their kills up trees which increases the chance of contact, and spotted hyaena tracks were often found with leopard tracks. Bothma and Le Riche (1984) suggest that the outcome of conflicts between leopards and spotted hyaenas depends on the sex and agressiveness of the leopard and the size of the hyaena pack. Contacts between a leopard and spotted hyaenas at a carcass in the Klaserie Private Nature Reserve were not known to be fatal. Pienaar (1969) records one case of a hyaena carrying the carcass of a fully-grown young leopard.

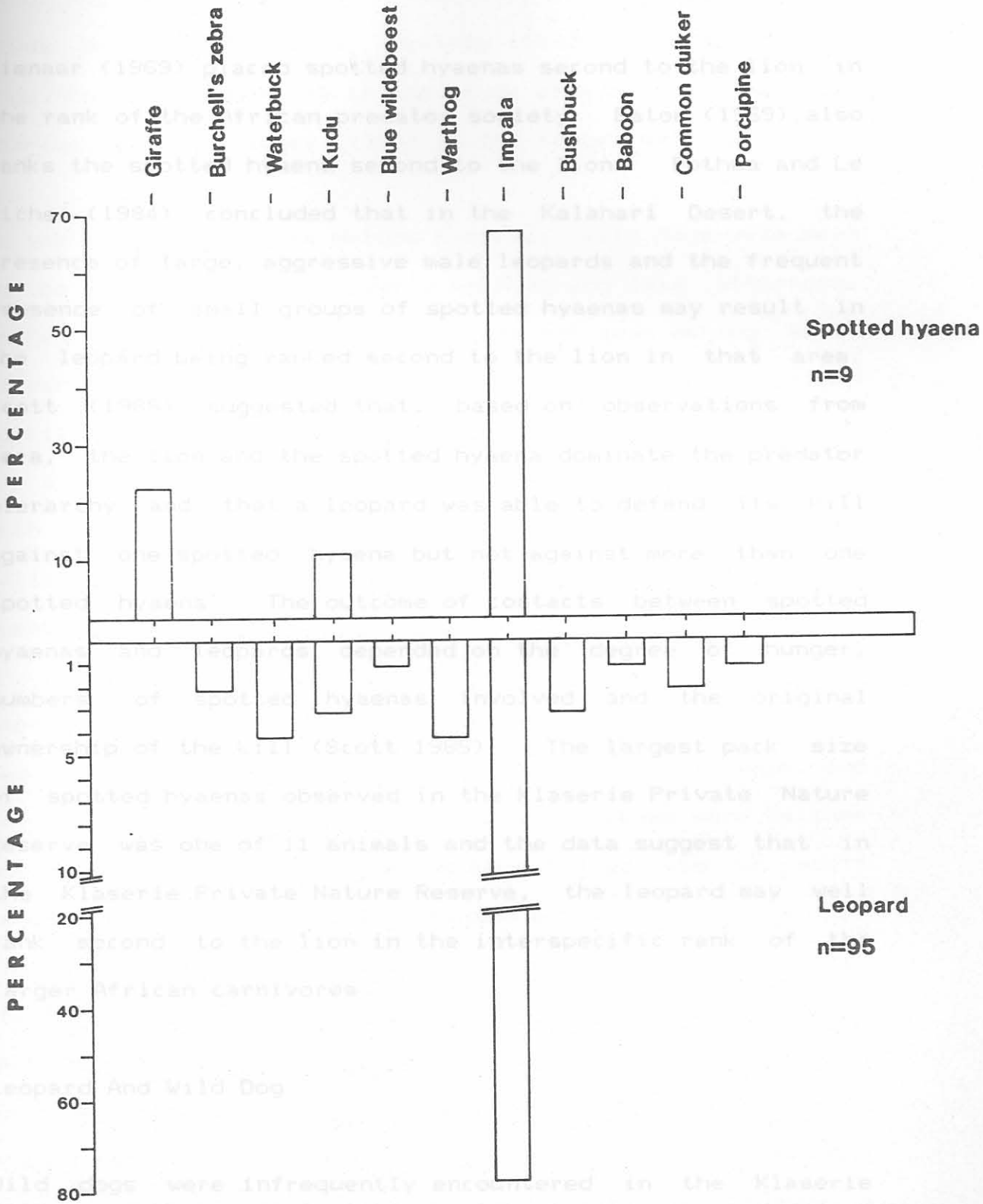

Figure 14: The percentage occurrence of different prey types in the diet of spotted hyaenas and leopards in the Klaserie Private Nature Reserve, Eastern Transvaal Lowveld, February 1979 to October 1981.

Bertram (1982) recorded leopards killing spotted hyaenas.

Pienaar (1969) placed spotted hyaenas second to the lion in the rank of the African predator society. Eaton (1969) also ranks the spotted hyaena second to the lion. Bothma and Le Riche (1984) concluded that in the Kalahari Desert, the presence of large, aggressive male leopards and the frequent presence of small groups of spotted hyaenas may result in the leopard being ranked second to the lion in that area. Scott (1985) suggested that, based on observations from Mara, the lion and the spotted hyaena dominate the predator hierarchy and that a leopard was able to defend its kill against one spotted hyaena but not against more than one spotted hyaena. The outcome of contacts between spotted hyaenas and leopards depended on the degree of hunger, numbers of spotted hyaenas involved and the original ownership of the kill (Scott 1985). The largest pack size of spotted hyaenas observed in the Klaserie Private Nature Reserve was one of 11 animals and the data suggest that in the Klaserie Private Nature Reserve, the leopard may well rank second to the lion in the interspecific rank of the larger African carnivores.

Leopard And Wild Dog

Wild dogs were infrequently encountered in the Klaserie Private Nature Reserve. It is accepted that their ranges

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