Multivariate analysis of the hunting tactics of Kalahari leopards

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The hunting tactics of male and female leopards in the southern Kalahari were analysed for prey-specific patterns. The field study was based on tracking leopard spoor in the sandy substrate of the Kalahari. Visual profiles for each type of prey were compiled for various facets of hunting. Data sets were analysed further, using Correspondence Analysis and Detrended Correspondence Analysis. The results indicate that multivariate analysis can be used to demonstrate prey-specific hunting tactics in Kalahari leopards. In using a scarce prey base, Kalahari leopards seem to be number maximisers as they are unselective of prey type, age or sex. The presence of prey-specific hunting tactics may indicate a move along a continuum towards some degree of energy maximisation.

Keywords: Kalahari; leopard; *Panthera pardus*; hunting tactics; multivariate analysis.

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Introduction

The leopard *Panthera pardus* occurs widely (Wozencraft 1993) and lives in forest, savanna, scrubland or desert (Smithers 1983). The secretive nature of the leopard has precluded in-depth studies of the hunting behaviour of this large, solitary, nocturnal carnivore (Bailey 1993).

The successful existence of any predator depends largely on the quality and quantity of its food (Griffiths 1975). Natural selection in carnivores shapes and refines predatory strategies to maximise the nutrient intake within the limits of ecological constraints. These constraints may differ widely within the same species at the geographical extremes of its range (Sunquist & Sunquist 1989; Karanth & Sunquist 1995). In desert or arid environments where ecological constraints are more stringent, it can be expected that the hunting tactics of a predator will be refined for survival. This adaptation may also be influenced by a prey base which varies in behaviour, numbers and distribution (Eltringham 1979).

The characteristics of a prey population also play a vital role in shaping a predator's hunting behaviour in a given area (e.g. Schaller 1972a, 1972b; Kruuk 1986; Bothma & Le Riche 1989; Sunquist & Sunquist 1989; Bailey 1993; Karanth & Sunquist 1995). Recent studies have shown that prey availability, abundance, size, vulnerability and behavioural response to predation are all important in this regard (Kruuk 1986; Sunquist & Sunquist 1989; Karanth & Sunquist 1995). Prey response to hunting pressure may include either flight or aggression, and necessitates a predator to exploit every possible opportunity to achieve a successful hunt (Schaller 1972a, 1972b; Bothma & Le Riche 1989).

While prey abundance influences the frequency of possible hunts, prey availability refers to the chances of encountering and successfully killing a specific prey (Kruuk 1986). Prey size is important as it relates to the balance between energy expenditure and gain during the hunting process. For example, smaller, but more abundant prey may be more profitable to hunt than larger and often less abundant prey (Sunquist & Sunquist 1989). Prey vulnerability indicates the prey's ability to escape when targeted and it is another characteristic which may shape the hunting behaviour of a predator. The modal prey size of large felids is considered to be most strongly influenced by prey availability and prey vulnerability (Sunquist & Sunquist 1989). Prey vulnerability depends to some degree on anti-predatory defense mechanisms and it is necessary to study such an aspect in various felid habitats (Kruuk 1986). Some predators select for prey digestibility and nutrient quality and hence these factors may also influence hunting behaviour. However, their importance in shaping the hunting behaviour of felids is less likely because felids have stable and efficient digestive systems (Sunquist & Sunquist 1989).

The hunting techniques of leopards in the Kalahari vary greatly and stalking does not appear to be as prominent as elsewhere within its range (Bothma & Le Riche 1984, 1989). Hunger is a primary hunting motivation, but all prey encountered are usually hunted. In leopards, increasing hunger is directly proportional to distances covered, so as to increase the chances of potential hunts (Bothma & Le Riche 1990). The prey base in the southern Kalahari, although adequate, is limited especially when compared to that available to leopards in some tropical forests where prey densities can be as high as 91 animals per km² (Karanth & Sunquist 1995). Scat analysis shows that Kalahari leopards do not hunt for murid rodents (Bothma & Le Riche 1994a) as was found in Zimbabwe (Grobler & Wilson 1972). Prey availability, not hunting cover, seems to be the most severe restriction for successful hunting by leopards in the Kalahari (Bothma *et al.* 1994). Due to the size and remoteness of the area and the many smaller, nocturnal prey available, no realistic assessment of prey densities in the Kalahari is possible (Bothma *et al.* 1994). Ambient temperature also affects the movements and hunting efforts of leopards, with the shortest distances covered during hot, summer months and the longest during cold, winter months (Bothma & Le Riche 1994b).

The hunting and kill rates of Kalahari leopards clearly reflect prey availability, abundance and vulnerability (Bothma & Le Riche 1984, 1986, 1989). It may therefore be expected that there would be prey-specific patterns of hunting behaviour, especially stalking and chase distances, percentage contribution of a prey to all hunts and kills, as well as the number of kills per hunt or the number of hunts required to make a kill. If hunting tactics prove to be prey-specific, it is possible that prey species with similar flight behaviour, availability, abundance, size and vulnerability may elicit similar hunting tactics from Kalahari leopards. As male (60 kg) and female (32 kg) leopards differ considerably in body size (Smithers 1983), it is also possible that the sexes may differ in their hunting tactics.

Since it is difficult to measure the effect of prey characteristics on predator behaviour (Sunquist & Sunquist 1989), the suitability of multivariate ordination techniques (commonly used in plant ecology) to describe the predator-prey relationships, were investigated. The multivariate techniques were used to analyse the hunting tactics (profiles) of the Kalahari leopard based on five aspects of hunting behaviour, and to compare the hunting tactics for different prey.

Study area

The study was undertaken in the interior areas (away from the riverbeds) in the northern part of the Kalahari Gemsbok National Park (9 593 km²) of South Africa (Fig. 1). The study area covers about 3 000 km² and is an arid, open landscape of dunes and sandy savanna located in the southwestern corner of the Kalahari. Numerous mammals, birds and reptiles occur in the area and the relatively small mammals are potential prey for the leopard (Bothma & Le Riche 1984). The prey base varies annually and seasonally and is seldom abundant. The park, on average, receives less than 250 mm of rain per year and the rainfall decreases from the northeast to southwest (Van Rooyen *et al.* 1988). The vegetation is described in more detail by Leistner & Werger (1973) and Van Rooyen *et al.* (1988, 1994).

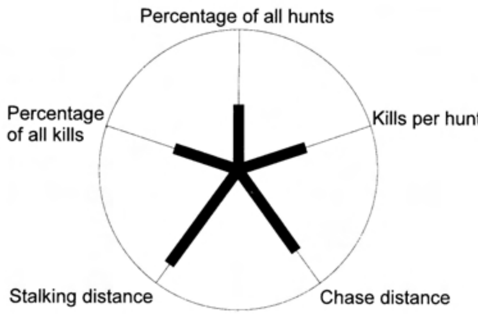

Fig. 2. Stylised hunting profile consisting of a rosette with five arms, each arm representing one of the aspects of hunting analysed.

Materials and methods

Field study

The tracks of leopards of known sex were followed on the sandy substrate of the park, with the aid of expert trackers, to document and interpret hunting behaviour (Bothma & Le Riche 1984). Tracking was done daily on various field trips, each lasting from 10 to 14 days from 1976 to 1992. Data for female leopards are based on 66 days of observation and 729.6 km of tracking, while that for males are based on 113 days of observation and 1961.1 km of tracking. Since the leopards were not marked, it is not known how many different individuals were involved. Details of the tracking technique appear in Bothma & Le Riche (1984, 1989).

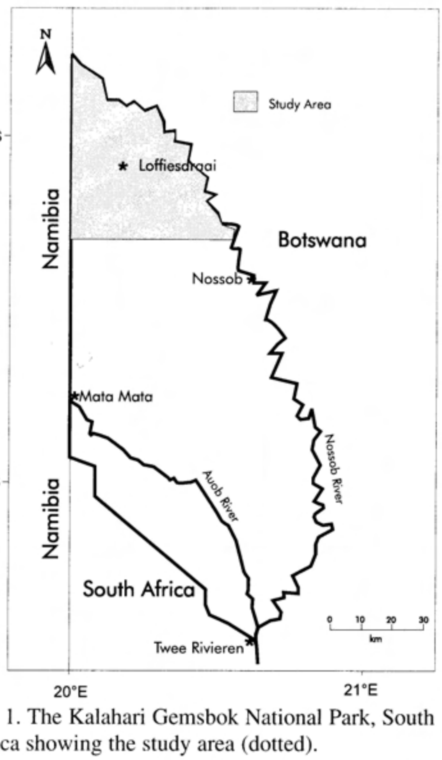

Fig. 1. The Kalahari Gemsbok National Park, South Africa showing the study area (dotted).

Analyses

Hunting behaviour by leopards in the Kalahari were analysed for the following prey: the gemsbok *Oryx gazella* (mainly calves and subadults), red hartebeest *Alcelaphus buselaphus* (mainly calves and subadults), springbok *Antidorcas marsupialis*, duiker *Sylvicapra grimmia*, steenbok *Raphicerus campestris*, aardvark *Orycteropus afer*, porcupine *Hystrix africaeaustralis*, Cape hare *Lepus capensis*, springhare *Pedetes capensis*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis*, aardwolf *Proteles cristatus* and the ostrich *Struthio camelus*.

Data for male and female leopards were initially separated. The following five aspects of hunting behaviour for each sex and prey type were analysed: the number of hunts on a particular prey expressed as a percentage of all hunts on all prey; the number of kills of a particular prey expressed as a percentage of the total number of kills of all prey; the number of kills per hunt per prey; the mean chase distance and the mean stalking distance for each type of prey. A hunting profile, hunting model or star symbol plot (Figs. 2 -5) was constructed diagrammatically for

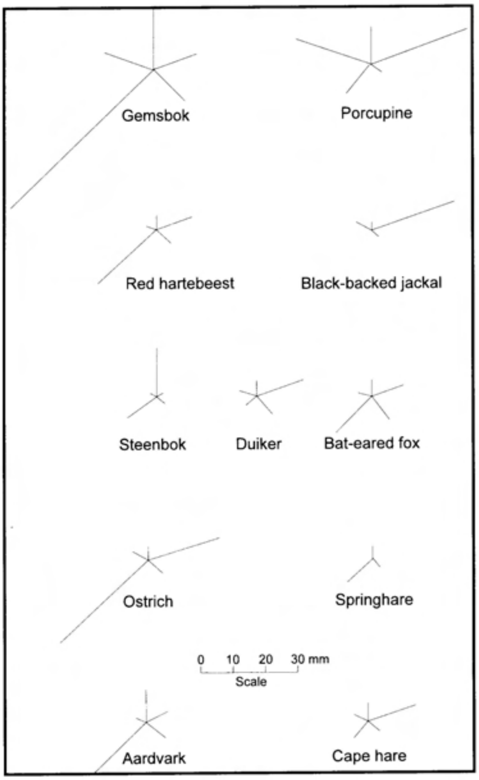

Fig. 3. Hunting profiles for major prey of male leopards in the southern Kalahari (also see Fig. 2).

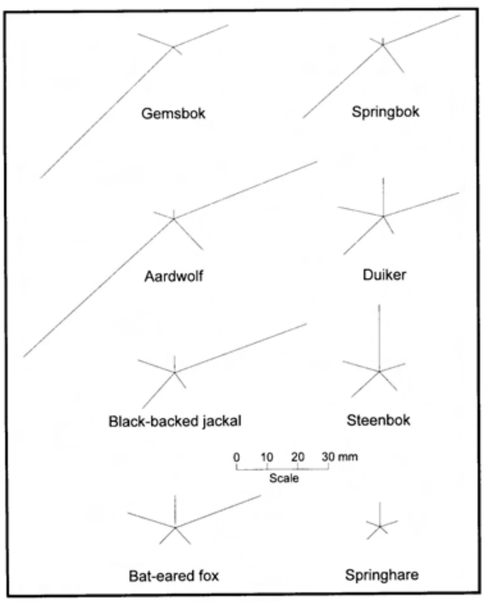

Fig. 4. Hunting profiles for major prey of female leopards in the southern Kalahari (also see Fig. 2).

each type of prey, for visual examination of similarities and differences. Each profile consisted of a star with five arms at equal angles, each arm representing one of the above aspects of hunting (Fig. 2). In constructing the profiles, the following scales were used: percentage of all hunts : 1 mm = 1 %; percentage of all kills: 1 mm = 1 %; chase distances: 1 mm = 5 m; stalking distances : 1 mm = 5 m and kills per hunt : 1 mm = 0.01. These scales were chosen arbitrarily for ease of visual presentation and comparison and are based upon the data in Tables 2-6.

The coded data were converted to linear measurements and were then used for the profiles (Figs. 3-5). The data were analysed further by using multivariate analysis techniques commonly used to study species/environment relationships (Kent & Coker 1992). Only prey for which sufficient data were available were included in the analysis. The hunting data for male and female leopards were analysed separately and in combination.

All data were first transformed to linear measurements as indicated above and arranged in a two-way table of rows (types of prey) and columns (aspects of hunting). These linear measurements were then analysed using Detrended Correspondence Analysis (DCA) and Correspondence Analysis (CA) of the CANOCO program (Ter Braak 1987). Hunting profiles were compared using all five variables simultaneously. In DCA, similar profiles will be positioned in close proximity in a two-dimensional space (scatter diagram).

Correspondence Analysis also provides a graphical display of data, but the distances between objects (types of prey) and variables (hunting aspects) are not critical (Beardall *et al.* 1986). However, the angle between two elements (e.g. prey animal and hunting aspect) and the origin gives an indication of the significance of their relationship. The acuteness of the angle is directly proportional to the degree of correlation. If the angle between the elements approaches 180° it is indicative of a strong negative correlation (Beardall *et al.* 1986). An element that plots close to the origin indicates a weak correlation.

Results

The prey base available in the study area is shown in Table 1, the actual hunting profiles appear in Figs. 3 - 5 and the field data appear in Tables 2 - 6.

Table 1
Daily abundance of potential ungulate and non-ungulate prey of southern Kalahari leopards counted during 2 628.1 km of tracking

Potential prey	*n*	Mean no. of animals per 10 km
Ungulate prey:		
Eland	60	0.20
Gemsbok	1183	4.50
Red hartebeest	420	1.60
Springbok	358	1.40
Duiker	120	0.50
Steenbok	693	2.60
Non-ungulate prey:		
Black-backed jackal	61	0.20
Bat-eared fox	24	0.10
Cape hare	147	0.60
Ostrich	127	0.50
All prey	3193	12.10

Prey size

The percentage distribution of 63 prey animals (based on modal mass) successfully hunted by male leopards and 28 prey by female leopards over a 16-year period is shown in Fig. 6. These results show that leopards in the Kalahari are opportunistic hunters which mainly target small to medium-sized prey, ranging in mass from 4 kg (bat-eared fox *Otocyon megalotis*) to 41 kg (adult springbok *Antidorcas marsupialis*).

Hunting profiles

The hunting profiles for male and female leopards are shown in Figs. 3 - 5. Male and female leopards hunted in the same area and used the same prey base. Hunting profiles for 11 types of prey of male leopards were constructed (Fig. 3) and eight for females (Fig. 4). Both sets of data show that various types of prey exhibited similar profiles, indicating the possibility of prey-specific hunting tactics. For some prey, there was no sexual dimorphism in hunting tactics (Fig. 5).

Detrended Correspondence Analysis

The detrended correspondence analysis separated prey species groups in which prey types were approached in a similar manner. Prey types of male leopards (Figs. 3 & 7) could be divided into the following groups: group 1 consisted of gemsbok, red hartebeest, ostrich, aardvark and bat-eared fox, while group 2 included the common duiker, Cape hare, black-backed jackal and porcupine. For the springhare and steenbok, males employed prey-specific tactics (Figs. 3 & 7). Prey types of female leopards could be divided into four distinct groups (Figs. 4 & 8). Group 1 included the common duiker, bat-eared fox and black-backed jackal; group 2 consisted of gemsbok, springbok, aardwolf, ostrich, porcupine and red hartebeest; group 3 included only steenbok and springhare; and group 4 the Cape hare and aardvark. Both males and females appeared to adopt the same hunting tactics for gemsbok, steenbok and black-backed jackals (Figs. 5 & 9).

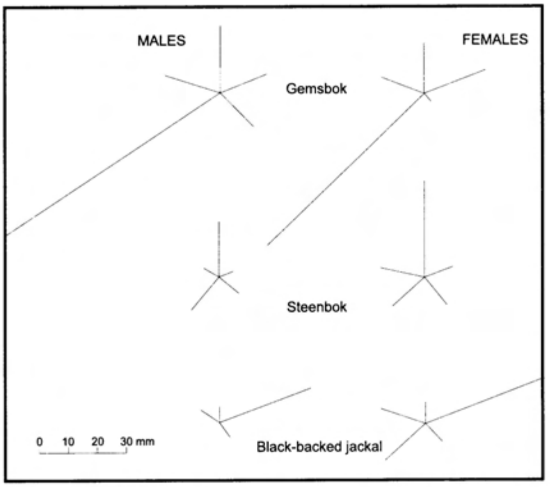

Fig. 5. Comparison of hunting profiles of prey which are similarly hunted by male and female leopards in the southern Kalahari (also see Fig. 13).

Table 2

Prey-specific hunting data for prey hunted by adult male (M) and female (F) leopards in the southern Kalahari, based on 113 days and 1961.1 km of spoor tracking for males and 66 days and 729.6 km for females

Prey	Hunts		% of all hunts		Kills		% of all kills		Hunts per kill		Kills per hunt	
	M	F	M	F	M	F	M	F	M	F	M	F
Eland	0	1	0.0	0.8	0	1	0.0	3.7	-	1.00	0.00	1.00
Gemsbok	66	17	23.1	13.7	11	4	20.8	14.8	6.00	4.25	0.17	0.24
Red hartebeest	14	2	4.9	1.6	2	0	3.8	0.0	7.00	-	0.14	0.00
Springbok	1	3	0.3	2.4	1	1	1.9	3.7	1.00	3.00	1.00	0.33
Duiker	17	15	5.9	12.1	3	5	5.7	18.5	5.67	3.00	0.18	0.33
Steenbok	55	36	19.2	29.0	2	4	3.8	14.8	27.50	9.00	0.04	0.11
Ostrich	11	2	3.8	1.6	3	0	5.7	0.0	3.67	-	0.27	0.00
Aardvark	31	2	10.8	1.6	2	0	3.8	0.0	15.50	-	0.06	0.00
Porcupine	44	2	15.4	1.6	16	0	30.2	0.0	2.75	-	0.36	0.00
Springhare	7	11	2.4	8.9	0	1	0.0	3.7	-	11.00	0.00	0.09
Cape hare	11	9	3.8	7.3	2	0	3.8	0.0	5.50	-	0.18	0.00
Aardwolf	0	3	0.0	2.4	0	2	0.0	7.4	-	1.50	0.00	0.67
Black-backed jackal	9	7	3.1	5.6	3	4	5.7	14.8	3.00	1.75	0.33	0.57
Bat-eared fox	18	14	6.3	11.3	2	5	3.8	18.5	9.00	2.80	0.11	0.36
Genet	1	0	0.3	0.0	5	0	9.4	0.0	0.20	-	5.00	-
Lizard	1	0	0.3	0.0	1	0	1.9	0.0	1.00	-	1.00	-
All prey	286	124	100.0	100.0	53	27	100.0	100.0	5.40	4.59	0.19	0.22

Table 3

Prey-specific stalking distances (m) of adult male leopards in the southern Kalahari based on 113 days and 1961.1 km of spoor tracking. Zero stalking distances (no stalking) were excluded from the analyses

Prey	Stalks ending in a kill			Unsuccessful stalks			All stalks		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Gemsbok	8	467.90	1185.20	49	345.60	491.59	57	365.60	625.38
Red hartebeest	2	7.50	6.36	11	170.10	279.26	13	145.10	262.15
Duiker	1	17.00	-	9	38.90	27.13	10	36.70	26.50
Steenbok	2	27.50	31.82	38	72.00	70.51	40	69.80	69.56
Ostrich	0	-	-	6	225.80	301.62	6	225.80	301.62
Aardvark	2	52.50	67.18	13	157.20	179.46	15	143.20	171.12
Porcupine	4	37.50	44.81	24	73.70	80.02	28	68.50	76.45
Springhare	0	-	-	4	57.50	30.69	4	57.50	30.69
Cape hare	1	13.00	-	5	33.40	25.84	6	30.00	24.57
Bat-eared fox	0	-	-	4	85.00	78.42	4	85.00	78.42
Polecat	0	-	-	1	9.00	-	1	9.00	-

All stalks: 10.9 % ended in kills (n = 184)

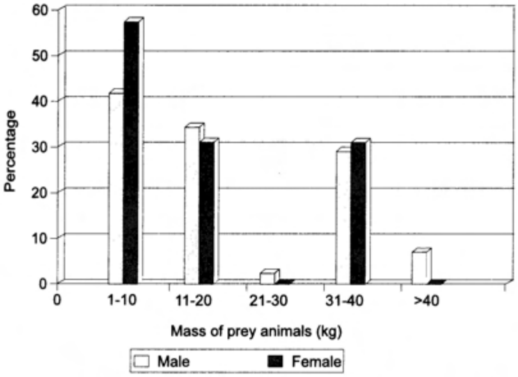

Fig. 6. Modal mass (kg) of male and female leopard prey in the southern Kalahari (males n = 63 kills; females n = 28 kills)

A comparison of male and female hunting tactics combined for all types of prey (Fig. 10) showed a distinct difference in hunting behaviour between the two sexes for some prey. However, certain types of prey, those that form groups as shown in Fig. 11, are hunted in a similar way by male and female leopards (e.g. steenbok and springhare).

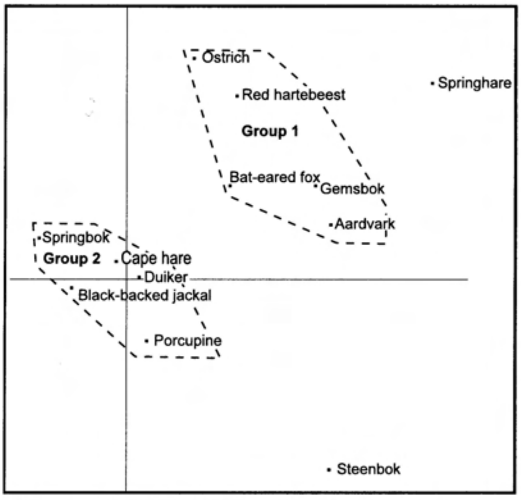

Fig. 7. Ordination diagram of prey hunted by male leopards based on Detrended Correspondence Analysis (DCA). (Eigen1 = 0.39; eigen2 = 0.05; scaling = -1).

Correspondence Analysis

The results of Correspondence Analysis appear in Figs. 12 - 14. From the analyses of the combined data, it is evident (Fig. 12) that there is some separation in the distribution of the hunting tactics between male and females. Therefore males and females have different general hunting tactics. The angle between elements and the origin shows that hunting by male leopards can be characterised by: a relatively high percentage of kills of porcupines; a high percentage of hunts (and long chase distances) for steenbok and springhare; a long stalking distance for the gemsbok, red hartebeest and the aardvark, with no stalking of the black-backed jackal; and a low frequency of hunting directed at the springbok and aardwolf. Hunting by females (Fig. 12), in contrast, shows a low percentage of kills of porcupines and ostriches when hunted (most animals hunted are not caught and killed); a high percentage of kills of the bat-eared fox and duiker; a high kill success (kills per hunt) for the black-backed jackal and aardwolf (most animals hunted are caught and killed); and a high percentage of hunting efforts directed at the steenbok and springhare.

The hunting tactics of male and female leopards were then analysed separately using Correspondence Analysis. Results for males (Fig. 13) show that the steenbok, and to a lesser extent the gemsbok and porcupine, are hunted often. The gemsbok, red hartebeest, ostrich, aardvark, springhare and bat-eared fox are all stalked and chased over longer distances than other prey. The ostrich and red hartebeest contribute little to the overall hunt and kill percentages, and thus to food gain. The springbok, black-backed jackal and Cape hare show a high kill success (kills per hunt) (most individuals hunted are also caught and killed).

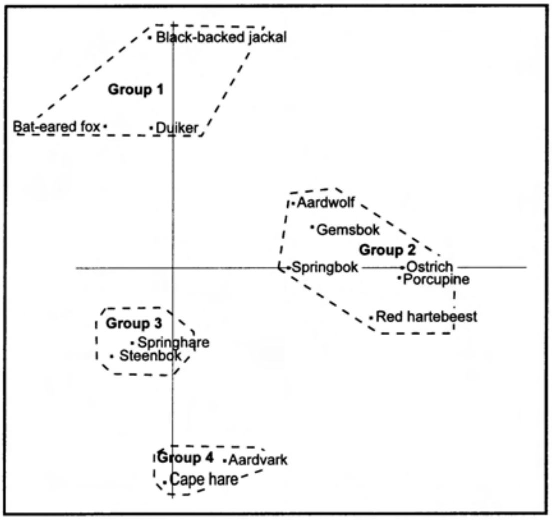

Fig. 8. Ordination diagram of prey hunted by female leopards in the southern Kalahari based on Detrended Correspondence Analysis (DCA). (Eigen1 = 0.34; eigen2 = 0.06; scaling = -1).

Results for females (Fig. 14) show that the Cape hare, steenbok and springhare are subjected to a high degree of hunting pressure. The springbok and aardwolf experience low hunting pressure, and there is a high kill success (kills per hunt) for the black-backed jackal. The duiker and bat-eared fox form a high percentage of kills, but these prey are also chased over long distances. Hunts on ostrich, gemsbok and porcupine show long stalking distances.

Prey-specific hunting

When the different types of prey were analysed for an overall hunting approach, the following was evident (Tables 2 - 6) (Figs. 3 - 9):

The gemsbok is hunted frequently by males, but this entails long stalking and chase distances and a low kill success (kills per hunt) (Table 2). Females also show long stalking distances and low kill success (kills per hunt)s for gemsbok, but short chase distances. The red hartebeest is hunted and killed infrequently by males, and is also stalked over long distances, while females seldom hunt red hartebeest.

Males and females hunt springbok infrequently but effectively when they

Table 4

Prey-specific chase distances (m) of adult male leopards in the southern Kalahari based on 113 days and 1961.1 km of spoor tracking. Zero chase distances (no chasing) were excluded from the analyses

Prey	Chases ending in a kill			Unsuccessful chases			All chases		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Gemsbok	7	78.60	120.87	23	81.70	87.33	30	81.00	93.86
Red hartebeest	2	31.50	111.02	4	21.50	27.11	6	44.80	64.90
Duiker	2	27.00	32.52	6	52.20	74.78	8	45.90	65.43
Steenbok	1	180.00	-	26	30.70	45.62	27	36.30	53.16
Ostrich	0	-		4	33.80	20.56	4	33.80	20.56
Aardvark	2	28.00	31.11	19	40.50	22.04	21	39.30	22.36
Porcupine	3	12.70	13.28	10	14.70	13.90	13	14.20	13.23
Springhare	0	-	-	3	17.30	19.66	3	17.30	19.66
Cape hare	1	26.00	-	4	23.00	12.36	5	23.60	10.78
Black-backed jackal	2	22.00	18.38	6	16.00	12.05	8	17.50	12.64
Bat-eared fox	0	-	-	12	54.40	89.56	12	54.40	89.56

All chases: 14.6 % ended in kills (n = 137).

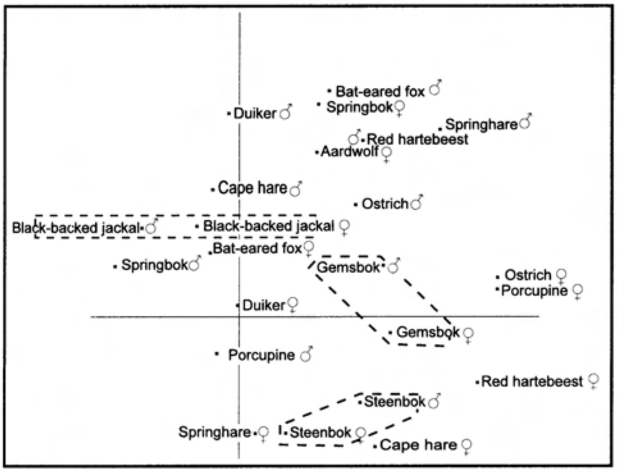

Fig. 9. Ordination diagram (DCA) of individual prey hunted by male and female leopards separately, based on five hunting aspects (Fig. 2). (Eigen1 = 0.32; eigen2 = 0.04; scaling = -1).

do (high kill success or kills per hunt) (Table 2). The duiker was hunted less frequently by males than by females. Male leopards usually kill duikers and black-backed jackal without the prelude of a stalk or chase (Bothma & Le Riche 1984; 1986). This behaviour results in a high kill success (kills per hunt), although a lower one than for females. The steenbok is hunted frequently by both males and females, but males are less successful in catching and killing them (low kill success or kills per hunt).

The ostrich is hunted and killed infrequently by both males and females. It is also stalked over long distances by both males and females. No chase data are available on ostriches for females, but males chased ostriches over long distances. The aardvark was hunted by males but seldom by females. When hunting aardvark, males stalked them over long distances. The porcupine was hunted and killed frequently by males, but seldom by females. Males also chased porcupines over short distances.

Table 5

Prey-specific stalking distances (m) of adult female leopards in the southern Kalahari based on 66 days and 729.6 km of spoor tracking. Zero stalking distances (no stalking) were excluded from the analyses

Prey	Stalks ending in a kill			Unsuccessful stalks			All stalks		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Gemsbok	2	462.50	576.29	7	346.00	535.36	9	371.90	509.03
Red hartebeest	0	-	-	2	45.00	7.07	2	45.00	7.07
Springbok	1	100.00	-	2	257.50	342.95	3	205.00	258.99
Duiker	0	-	-	7	92.00	63.78	7	92.00	63.78
Steenbok	1	50.00	-	22	67.00	71.35	23	66.30	69.80
Ostrich	0	-	-	2	553.50	772.87	2	553.50	772.87
Cape dikkop	0	-	-	1	12.00	-	1	12.00	-
Aardvark	0	-	-	1	7.00	-	1	7.00	-
Porcupine	0	-	-	1	240.00	-	1	240.00	-
Springhare	0	-	-	6	28.20	17.38	6	28.20	17.38
Cape hare	0	-	-	2	17.50	13.44	2	17.50	13.44
Black-backed jackal	1	85.00	-	0	-	-	1	85.00	-
Bat-eared fox	1	30.00	-	3	51.00	11.53	4	45.80	14.10
Aardwolf	0	-	-	1	400.00	-	1	400.00	-

All stalks: 9.5 % ended in kills (*n* = 63)

Table 6
Prey-specific chase distances (m) of adult female leopards in the southern Kalahari based on 66 days and 729.6 km of spoor tracking. Zero chase distances (no chasing) were excluded from the analyses

Prey	Chases ending in a kill			Unsuccessful chases			All chases		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Gemsbok	2	7.00	0.00	3	30.30	17.04	5	21.00	17.56
Springbok	1	100.00	-	1	30.00	-	2	65.00	49.50
Duiker	4	11.00	6.38	6	50.00	35.66	10	34.40	33.55
Steenbok	1	2.00	-	13	55.50	103.32	14	51.60	100.29
Aardvark	0	-	-	1	5.00	-	1	5.00	-
Porcupine	0	-	-	1	1.00	-	1	1.00	-
Springhare	1	15.00	-	4	12.80	12.09	5	13.20	10.52
Cape hare	0	-	-	7	13.40	13.01	7	13.40	13.01
Black-backed jackal	4	46.00	40.80	3	26.00	16.37	7	37.40	32.19
Bat-eared fox	3	15.00	11.79	3	83.70	28.29	6	49.30	42.31
Aardwolf	1	100.00	-	1	50.00	-	2	75.00	35.36

All chases: 27.9 % ended in kills ($n = 61$)

No males were observed hunting aardwolf in this study. Although hunted infrequently by females, they were killed often (high kill success or kills per hunt) when hunted. The black-backed jackal was hunted by males and females and, when done, it was killed frequently (high kill success or kills per hunt) by both sexes of leopard. The bat-eared fox was hunted frequently by females, but less so by males. Females caught and killed bat-eared foxes more successfully (high kill success or kills per hunt) than males.

The springhare is abundant in the Kalahari and was hunted frequently, especially by females. When hunted by males, they were stalked over long distances. The Cape hare was hunted frequently by females, but less so by males.

Discussion

Although large felids are generally considered to be opportunistic predators (Kruuk 1986), catching their prey from an ambush and/or a stalk and chase (Sunquist & Sunquist 1989), the specific hunting tactics used by Kalahari leopards vary from prey to prey (Bothma & Le Riche 1984, 1986, 1989). A solitary predator shows behavioural specialisations such as hunting prey of a modal size smaller than its own, and killing smaller prey more often than larger prey, which makes it successful at obtaining food (Sunquist & Sunquist 1989).

The results (Figs. 3 - 14; Tables 2 - 6) show prey-specific hunting tactics by male and female Kalahari leopards. Although some prey such as gemsbok and steenbok were hunted in a similar manner, males and females usually differed in hunting tactics, with various prey types being hunted differently. Females also generally stalk their prey over longer distances than males.

The gemsbok is abundant in the Kalahari (Table 1) and mainly calves were killed, although adults can also be taken. It was therefore, hunted frequently by all leopards, but especially so by the considerably larger males. Since a gemsbok can resist an attack when a calf is attended by a cow or is in a herd, they are stalked over long distances by all leopards so as to achieve optimal posi-

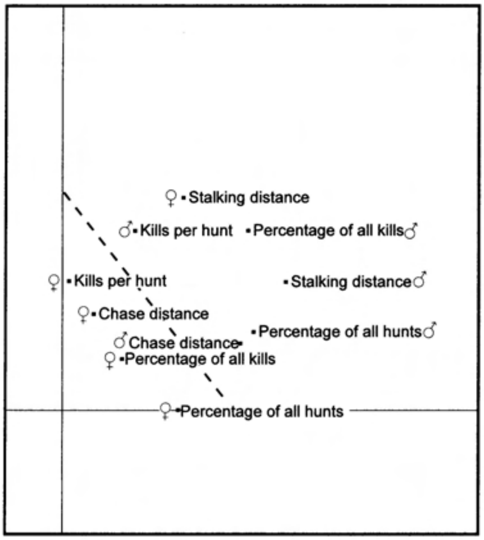

Fig. 10. Ordination diagram of five hunting aspects (Fig. 2), for male and female leopards combined, based on Detrended Correspondence Analysis (DCA). (Eigen1 = 0.28; eigen2 = 0.15; scaling = -1).

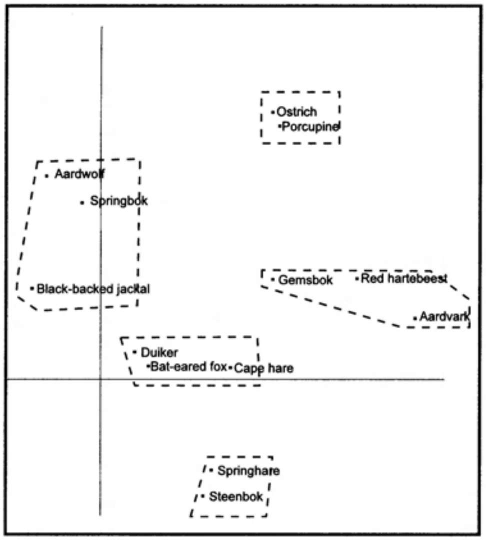

Fig. 11. Ordination diagram (DCA) of prey hunted by male and female leopards combined (Fig. 2) based on five hunting aspects. (Eigen 1 = 0.28; eigen2 = 0.15; scaling = -1).

tioning for the kill (Bothma & Le Riche 1989).

The red hartebeest occurs infrequently in the study area (Table 1). Consequently it was also hunted infrequently, but when hunted, males stalked them over long distances (Fig. 3; Table 3). This antelope is known to be vigilant with a keen sense of sight, and vigilance may here act as an anti-predator defense mechanism. Being a fleet-footed prey, it is uncertain why males indulge in long chase distances of this antelope, unless it is an attempt to secure the benefits of a large prey item (Sunquist & Sunquist 1989).

The springbok also occurs infrequently in the study area (Table 1) and was accordingly hunted infrequently. The common duiker was usually hunted and killed opportunistically, often being surprised and killed with no stalk and chase prelude (Bothma & Le Riche 1984, 1986). The smaller female leopard was more effective in killing duiker than the larger male, possibly because the female can stalk more secretively in the somewhat sparse hunting cover available (Figs. 3, 4 & 12). Duikers possess no obvious anti-predator defense mechanisms.

The small steenbok is an abundant antelope (Table 1) which is hunted often by all leopards (Fig. 5). Male and female leopards show similar hunting tactics towards steenbok. However, of all prey used by leopards in the Kalahari it seems to be the most difficult to catch, probably because of its vigilance and its fleet-footed flight response. In terms of its size and difficulty of catching, its continued hunting by leopards is probably due to its abundance and the fact that Kalahari leopards cannot afford to be highly selective of prey. Low prey densities require leopards in the Kalahari to hunt every potential prey animal encountered, even though the chances of success may be slim (Bothma & Le Riche 1990). Furthermore, males are at a disadvantage due to their greater size than females.

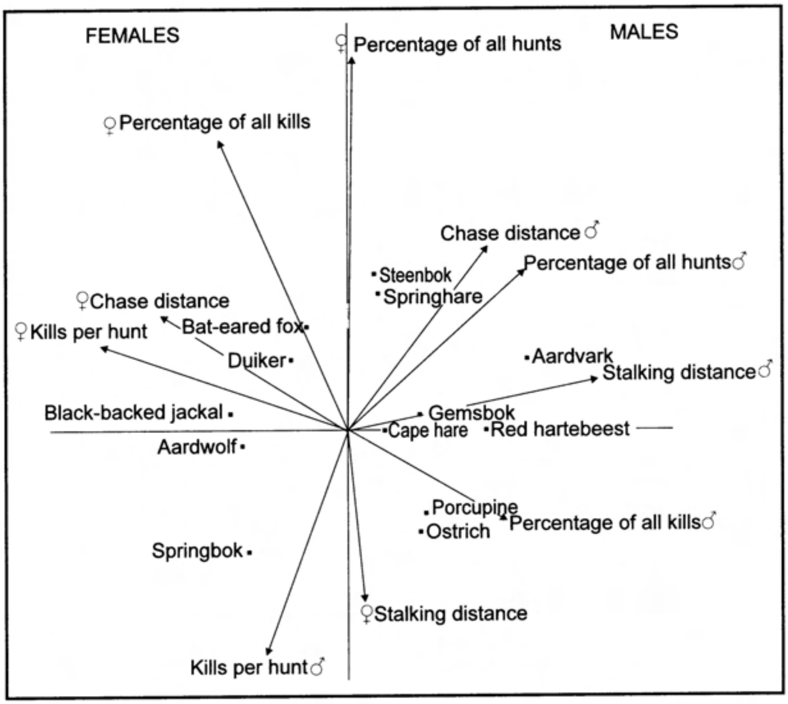

Fig. 12. Ordination diagram of prey and five hunting aspects (Fig. 2) for male and female leopards combined, based on Correspondence Analysis (CA). (Eigen1 = 0.28; eigen2 = 0.21; scaling = 2).

The ostrich is not abundant in the Kalahari (Table 1) and its long neck and keen eyesight may make it a difficult prey to stalk and catch, although the male leopard has some success in killing young ostriches (Table 2). The long stalking distances involved probably reflect an effective anti-predator mechanism.

The aardvark is fairly abundant in the Kalahari. It is hunted frequently by male leopards but it is unclear why females hunt them so seldomly. When hunted, they are stalked over long distances, probably due to their keen sense of hearing. It is also unclear why the abundant porcupine is hunted seldomly by females, but frequently by males. When disturbed, porcupines often do not flee but go into a defensive stance with the quills raised in a protective screen. This defensive reaction is probably why they are seldom targeted.

Of the smaller carnivores, no reliable counts were possible. However, the aardwolf is hunted infrequently and with no real defense mechanisms, it is easily caught and killed by especially female leopards (Fig. 4). The black-backed jackal is abundant in the Kalahari, but is hunted infrequently. This is a vigilant and fleet-footed carnivore, but its habit of following and barking at large predators, and its attraction to kills makes it vulnerable (high kill success or kills per hunt, Table 2). The bat-eared fox, with its large ears, has a keen sense of hearing, but its slow speed over long distances makes it vulnerable. However, by making quick, sharp turns when fleeing, bat-eared foxes are able

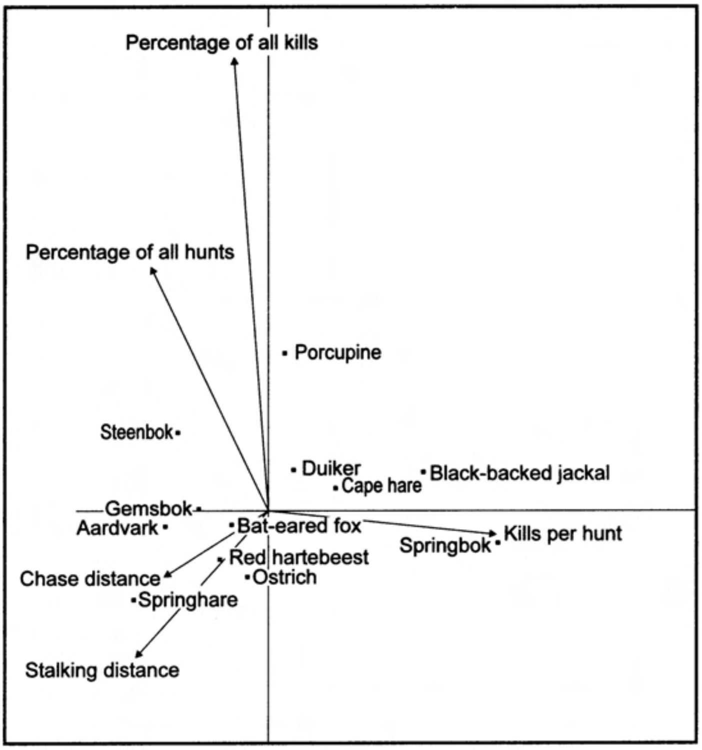

Fig. 13. Ordination diagram of the prey and five hunting aspects (Fig. 2), for male leopards in the southern Kalahari, based on Correspondence Analysis (CA). (Eigen1 = 0.39; eigen2 = 0.10; scaling = 2).

to elude larger male leopards more easily than the smaller and more agile females.

The springhare has a keen eyesight and is abundant in the Kalahari. It is stalked and chased over long distances, especially by the larger males, but yields a low kill success or kills per hunt. The fleet-footed Cape hare is also abundant in the Kalahari (Table 2) but possibly due to its small size, which limits detection from a distance, it is often simply chased without being stalked first.

Although hunting cover for leopards in the Kalahari is sufficient (Bothma *et al.* 1994) the area is fairly open and the vegetation somewhat sparse, particularly during droughts. This may be one reason why the larger male leopards revert to stalking different types of prey over longer distances than the females, which are of smaller stature and hence can approach prey closer under protection of the available cover. The total prey spectrum taken by all leopards, may reflect the validity of Sunquist & Sunquist's (1989) views that large, solitary felids will tend to take prey of a modal size which is mostly less than their own body weight (Fig. 6). Female leopards in the Kalahari, however, take a large percentage of prey in the 31 - 40 kg category (Fig. 6), compared to their mean weight of 32 kg. Why this is the case, remains unknown.

In a study of the feeding ecology of the dingo *Canis lupus dingo* in an arid part of Australia (Corbett & Newsome 1987), concluded that dingoes adopt a feeding (hunt-

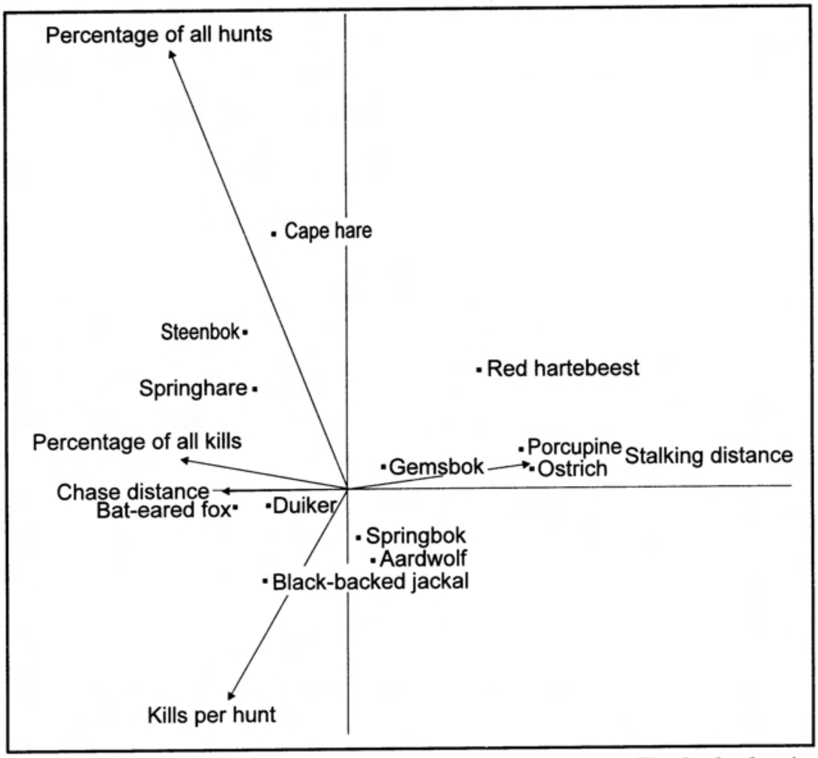

Fig. 14. Ordination diagram of the prey and five hunting aspects (Fig. 2), for female leopards in the southern Kalahari, based on Correspondence Analysis (CA). (Eigen1 = 0.34; eigen2 = 0.16; scaling = 2).

ing) strategy aimed at getting at least a threshold source of energy or nutrients in a capricious and arid environment where prey availability fluctuates greatly. The foraging behaviour of dingoes is considered to be a trade-off between foraging and other ecological requirements. This is consistent with all known foraging models, including optimal, sub-optimal, non-optimal foraging and their various extensions, which ultimately all involve only one model of effective foraging (Corbett & Newsome 1987). The same may apply to Kalahari leopards.

Leopards in the tropical forests in southern India, where there is an abundant prey base, hunt selectively for type, size and condition in some prey (Karanth & Sunquist 1995). These findings also support the prediction of Griffiths (1975) that vertebrate predators would be selective energy maximisers (selective predation) in prey-rich habitats, but would be non-selective number maximisers where large prey are scarce. The behaviour of southern Kalahari leopards in a prey-poor area lends further support for Griffith's (1975) prediction. Although Kalahari leopards are herein considered to be number maximisers as opposed to those of the tropical forests in southern India, where they are energy maximisers, they also sometimes adopt clear prey-specific hunting tactics. This may suggest evidence for movement towards energy maximisation. It is possible that adaptable predators such as the leopard may occupy variable positions in a foraging strategy continuum which ranges from number maximisation to energy maximisation, depending upon the habitat and the prey-base available. If true, then the constraints of the environment will ultimately determine the predation strategy adopted on that continuum.

Conclusions

Leopards in the southern Kalahari clearly show prey-specific hunting tactics. Males and females may have similar hunting tactics for certain prey species, but differ in prey taken and hunting tactics used for other species. These leopards appear to be number maximisers in terms of foraging strategy. Ordination techniques, normally used by plant ecologists, are useful to describe predator-prey relationships.

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