Foraging dynamics of lions in a semi-arid environment

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Direct observations on the foraging activities of lions, based on 920 attempts to capture prey and 156 kills, on the plains of Etosha National Park, Namibia, revealed a regular nocturnal pattern of mostly coordinated group hunting. Lions scavenged rarely and killed mainly prey animals weighing less than 50 kg, which contributed to 73% of the observed kills and 50% of the estimated biomass consumed. Capture success increased with lion group size and was also greater during coordinated group hunts. Lions hunted most of the prey that they encountered, showing a preference for large prey species. Average food acquisition ranged from 8.7 kg/day per lioness in the dry season to 14 kg/day per lioness in the wet season. During the dry season, coordinated cooperative hunting was essential and lionesses most often formed groups of 2, thereby acquiring higher daily food intake than groups of other sizes. In the wet season, lioness groups of all sizes obtained more than the estimated daily requirements, and lionesses did not uniformly forage in the smaller groups capable of greater food acquisition.

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L'observation directe de lions en chasse au cours de 920 tentatives de capture de proies et de 156 captures réussies, dans les plaines du parc national Etosha, Namibie, a révélé l'existence d'un cycle régulier nocturne de chasse, surtout organisée, en groupes. Les lions consommaient rarement des charognes et tuaient surtout des proies de moins de 50 kg, ce qui constituait 73% des mises à mort observées et 50% de la valeur estimée de la biomasse consommée. Le succès des captures augmentait en fonction du nombre de lions dans le groupe et augmentait aussi si les groupes étaient organisés. Les lions chassaient la plupart des proies qu'ils rencontraient et préféraient les grandes espèces de proies. La consommation moyenne de nourriture se situait entre 8,7 kg/jour par lionne au cours de la saison sèche et 14 kg/jour par lionne au cours de la saison humide. Pendant la saison sèche, la chasse organisée en groupes était essentielle et les lionnes formaient surtout des groupes de deux, arrangement qui leur fournissait la plus grande quantité quotidienne de nourriture. Durant la saison humide, les groupes de tous nombres obtenaient plus que la ration quotidienne essentielle estimée et les lionnes ne chassaient pas nécessairement en groupes de petits nombres propres à leur assurer le plus grande quantité de nourriture.

[Traduit par la rédaction]

Introduction

Predation by lions (*Panthera leo*), combined with disease, was identified by Berry (1980) as the major cause of a marked decline in the wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchellii*) populations in Etosha National Park during the 1970s. Wildebeest and zebra formed 80% of the lion's food items. Springbok (*Antidorcas marsupialis*), however, were little affected by predation, increasing by a factor of 3.3 between 1974 and 1978, despite high predator–prey ratios (1:72–105). It is well known that in studies of large carnivore predation based on carcase assessments, such as that by Berry (1981), small animals and the young of larger species are often underrepresented (Kruuk and Turner 1967; Pienaar 1969; Schaller 1972; Rudnai 1973; Eloff 1984; Mills 1990). Direct observations of foraging predators, as in studies by Schaller (1972), Kruuk (1972), Van Orsdol (1984), and Mills (1990), have reduced this bias.

The initial objective of the present study was to test Berry's hypothesis for the 1980s and to determine whether the abundant springbok formed an important part of the lions' diet on the plains of Etosha National Park (referred to as Etosha). From May 1984 to July 1988, I directly observed lions for a total of 3134 h and followed them for 1443 km to assess foraging behaviour, prey preference, hunting success, and food acquisition.

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Methods

Study area

Etosha National Park straddles the junction of three major biotic zones, the southern savanna woodland, the south-west arid, and the Namib desert (Smithers 1983), with its coordinates centering at 19°S, 16°E. Berry (1980) gave a detailed description of Etosha's history, climate, vegetation, geology, and management, and the following features are of interest to the present study. Etosha occupies an area of 22 270 km^2, with a mean annual rainfall of 351 mm. There is a wet season (January–May) and a dry season (June–December). The Etosha Pan (Fig. 1), a saline desert, is surrounded by short-grass plains (Le Roux *et al.* 1988) which compose less than 10% of Etosha's surface area. These plains form an important part of the grazing areas for an estimated 4300 zebra, 10 000 springbok, 2500 wildebeest, and 1500 gemsbok (*Oryx gazella*) (Gasaway *et al.* 1991). Migratory patterns of these plains ungulates have been described elsewhere (Berry 1980; Stander *et al.* 1990) and adhere to roughly the following pattern. During the dry season, ungulates are widely spread along the plains edging the southern and eastern half of the Etosha Pan. At the start of the rains (January–February) the ungulates move westwards and concentrate on the western plains of Etosha for the duration of the wet season. The 5 prides (9–15 lions; 1–4 adult males, 4–7 adult females, 0–3 subadults, 0–4 large cubs, and 0–6 small cubs) observed showed extended home ranges that included the ungulate concentration areas during the wet season (H. Berry, unpublished data).

In 1978, Berry (1981) estimated the lion density on the plains of Etosha at 15.9–22.2/100 km^2, and counted 21 prides. Ten years later, after the individual marking of over 150 lions (Orford *et al.* 1988; Stander 1991), the lion population in the whole of Etosha

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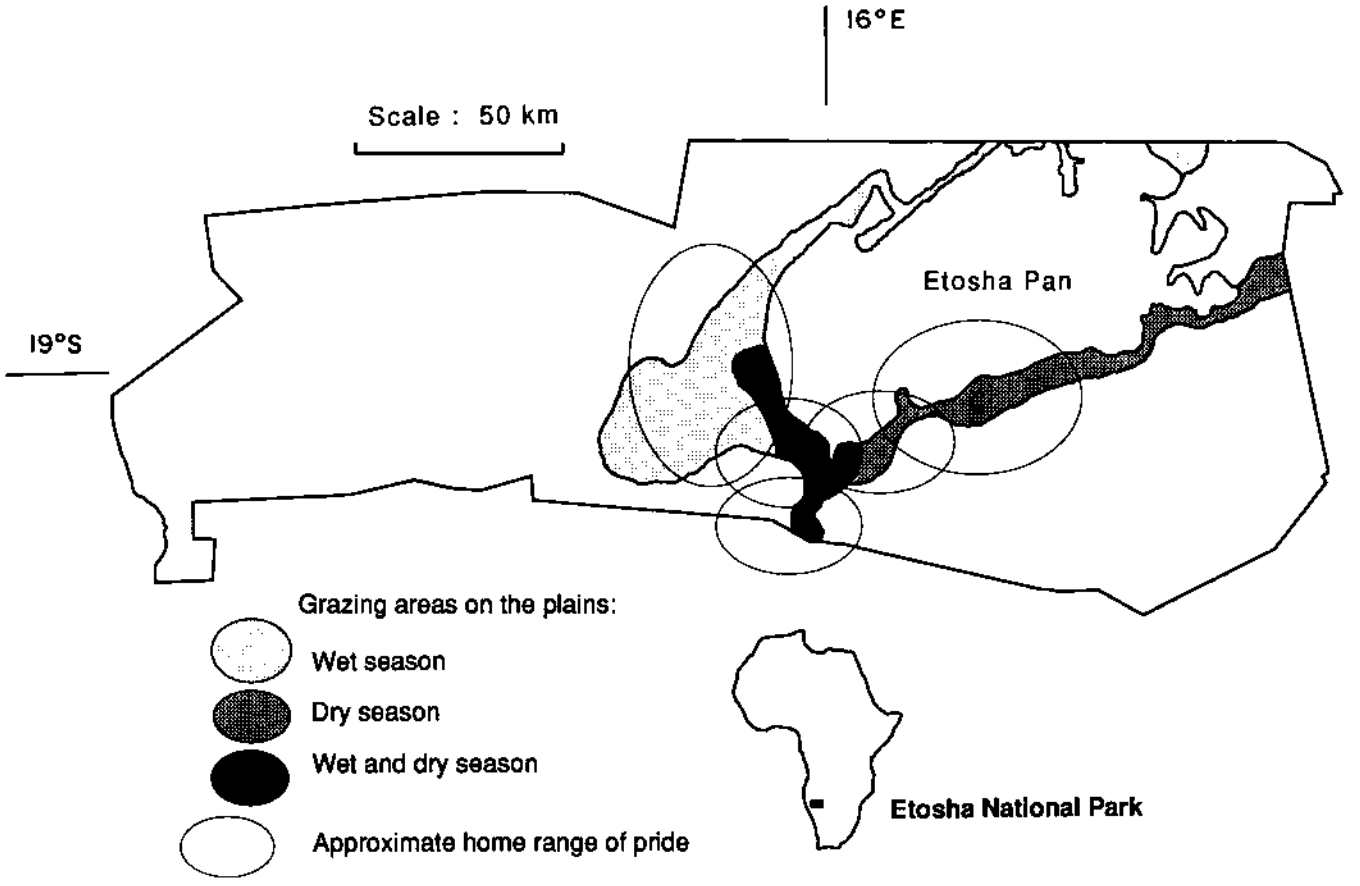

FIG. 1. Etosha National Park, Namibia, indicating the short-grass plains surrounding the Etosha Pan and the approximate home ranges of 5 prides that were frequently observed during the 4-year study period. The plains are the wet- and dry-season grazing areas for springbok, wildebeest, and zebra.

ranged between 1.6 and 2/100 km^2. The plains supported 2.8 lions/100 km^2, with 9 distinct prides. In addition, there were 5 spotted hyaenas/100 km^2 on the plains (Gasaway *et al.* 1989).

Identification, tracking, and observations

Most lions (n = 53) in the study area were immobilized (Van Wyk and Berry 1986; Stander and Morkel 1991) and permanently marked with a hot brand (Orford *et al.* 1988); three additional lionesses were individually recognizable from natural scars. All lions were classified in age categories as described by Schaller (1972). One to 3 lionesses in each of 5 prides were radio-collared. To avoid the bias of following the same subgroups, members of different subgroups were radio-collared. Lions were located by radiotelemetry, by following the direction of roars (Stander and Stander 1988) or by tracking their spoor. Observations were performed from a vehicle at distances of 20–100 m. A focal lioness was randomly selected for the duration of the observation period. Her behaviour and that of all lions associating with her were recorded. The focal lioness' associates often varied, owing to frequent regrouping.

Observation periods ranged between 1 day (24 h) and 15 days. During the heat of the day, when lions were inactive, I slept in the observation vehicle. At night, lions were viewed with image-intensifying night-glasses, or with low-light binoculars aided by a 75-W red-filtered spotlight, or with an infrared-sensitive video camera. The study area was subject to high tourist pressure, which was advantageous, as both lions and prey were habituated to the presence of vehicles. Care was taken, however, not to disturb the animals or to dazzle prey when the red-filtered light was used.

Scientists and park rangers in Etosha collected data on animal mortalities, with an emphasis on lion predation, based on the analysis of carcases as a part of their daily routine. These records for the period and area of the present study (Etosha Ecological Institute, unpublished data) were compared with my data. Wind direction was estimated at the beginning of hunts, and recorded in relation to the lions' initial approach to the prey (e.g., upwind, downwind, or with a cross-wind). Distance travelled was measured using the vehicles' odometer, and hunting and feeding times by means of a stopwatch.

Classification of hunts and definitions of terms

Several authors have mentioned the difficulty of defining a hunt (Kruuk 1972; Schaller 1972; Mills 1990). In the present study, foraging was defined as searching for and hunting prey, and feeding. The search for prey included all walking and running, even when the lions' intentions were unclear, as covering distance increased their chances of encountering prey (Elliot *et al.* 1977). Lions encountered prey when they were within sight of them, an estimated distance of 500 m. A "group" was defined as lions of the same pride who were within 200 m of each other (Packer *et al.* 1990). A lion or group of lions were considered to be "hunting" when, upon spotting prey, they stared at it with an alert posture and alert facial expression (Schaller 1972), and then at least one lion stalked the prey for more than 10 m, only abandoning the hunt when the prey escaped. Since some lions may not participate in group hunts (Scheel and Packer 1991), "participation" was defined as active stalking or crouching with an alert facial expression. "Ambush" was defined as the adopting of a crouching position from which a lion could catch prey fleeing from another lion, and "rush" was defined as a lion capturing prey after a chase of up to 150 m. "Hunting success" refers to the percentage of hunts resulting in a kill, and "food intake" to the estimated amount of food (kg) consumed per day by a lioness.

During the initial stages of the study, a rough map was drawn of all observed hunts, indicating the movements and positions of the

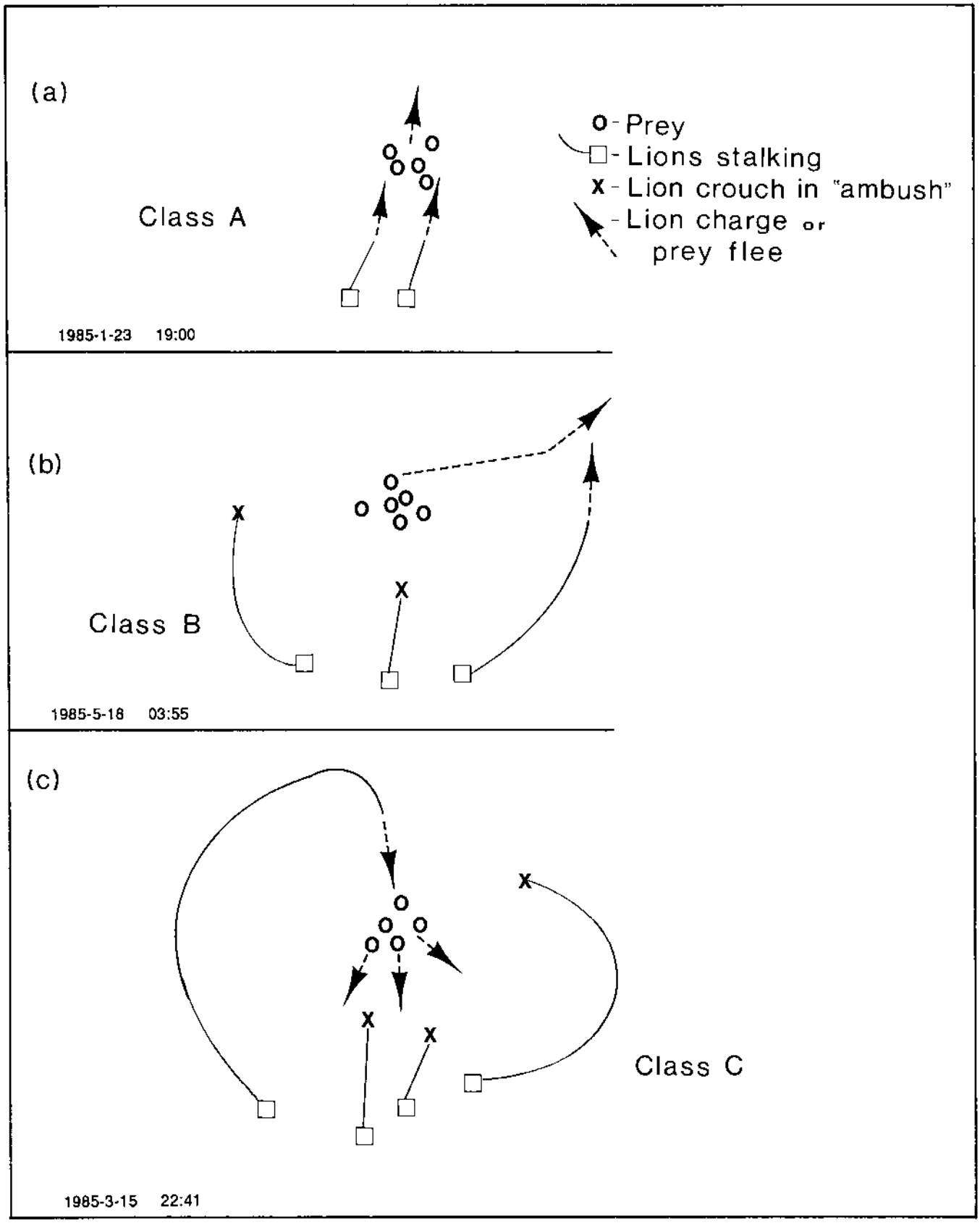

FIG. 2. Three hunts, indicating the stalking patterns of lions in relation to the prey and other lions, exemplifying the three hunt classes. In the class A example, two lions stalked directly at prey, with little coordinated cooperation. In the class B example, two lions attempted to encircle the prey while another waited in "ambush" position. Cooperation in this hunt may have been accidental, as one lion charged at the prey but this was unrelated to the activities or positions of the others. The class C example illustrates coordinated cooperation as one lion encircled the prey and charged. The prey then ran towards the other lions who were crouched in "ambush" positions.

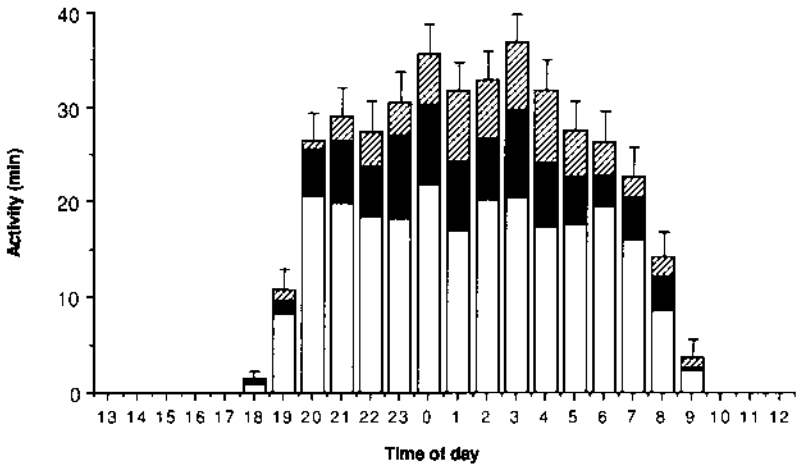

FIG. 3. Average foraging activity patterns of lions in Etosha National Park during 74 full 24-h periods. Search for prey (open bar), hunting (solid bar) and feeding (hatched bar) are presented as the average number of minutes of that activity per hour. The standard error values indicated refer to the mean duration of the combined activities per hour. The sun set between 18:30 and 19:30 and rose between 06:30 and 07:30.

lions and prey (n = 108; see Fig. 2, for example). On the basis of these diagrams 3 basic hunt classes were identified.

Class A: This hunt class involved a lion or group of lions stalking the prey directly and attempting to capture it after a relatively short chase, a method analogous to that used by Scheel and Packer's (1991) "conformists." When more than one lion was present, each approached the prey directly (Fig. 2*a*), showing little coordination.

Class B: This hunt class involved 2 or more lions stalking prey, some individuals attempting to encircle the prey while others waited in an ambush position or advanced slowly. This class of hunt usually ended when prey animals detected the stalking lions, or when a lion charged at the prey, apparently irrespective of the positions or activities of the other lions (Fig. 2*b*). Although this hunt class is similar to class C, the apparent coordinated cooperation may be explained as "accidental" (Kruuk and Turner 1967; Kruuk 1982) and is therefore treated separately for now.

Class C: These hunts involved a higher level of coordination than class B hunts. Upon spotting prey, some lions would fan out and encircle it while others waited or advanced slowly; all lions appeared to watch both the prey and other pride members and to adjust their own movements accordingly. The encircling lions usually charged at the prey, which would often run towards those in ambush (Fig. 2*c*). Class B and C hunts both appear to be similar to Scheel and Packer's (1991) "pursuing."

Grouping patterns and food consumption

Changes in the grouping patterns of the observed prides occurred at least once every 48 h and sometimes several times per night. Lions did not forage during the daytime, when group composition remained largely the same. Estimation of foraging group sizes was therefore based on the animals present during observed hunts rather than on direct measurement of the time spent in groups of each size.

The carcase mass of prey was estimated on the basis of mean live mass recorded for age and sex classes of each prey species (Smithers 1983; K. Panagis, personal communication; personal observations). The weight of food consumed was taken as the difference between the estimated live weight of prey and the estimated percentage of inedible parts (33% for animals >80 kg, 10% for animals 5–80 kg, and 0% for animals <5 kg; Mills 1990). The crudeness of this method is acknowledged. Daily food intake was measured per lioness, assuming that each carcase was divided equally among lionesses, as no social hierarchy exists among lionesses in a pride (Schaller 1972; Bertram 1978; Packer and Pusey 1985). Adult males ate twice as much, subadults equal amounts, and large cubs three-quarters as much as adult females (Van Orsdol 1982*b*). Meal sizes at each carcase were also adjusted when spotted hyaenas (*Crocuta crocuta*) robbed lions of their kill or when lions left a carcase prematurely. Daily food acquisition was calculated for adult and subadult females of each group size because all lionesses over the age of 18 months participated in hunts (Packer *et al.* 1990; this study).

TABLE 1. Numbers of lions present at and participating in 910 hunts in Etosha National Park

	No. of lions present	No. of lions participating	% nonparticipants
Males			
Adults	461	20	96
Subadults	90	10	89
Large cubs	204	0	100
Females			
Adults	3256	3233	1
Subadults	110	110	0
Large cubs	326	168	54

All lions <200 m apart were considered to be present, but only those that stalked or crouched and stared at prey with an alert facial expression were considered to be participants.

As with most behavioural studies, data could not be normalized and nonparametric statistics are used (Siegel 1956). All P values are two-tailed. Where possible, statistical means are given, with standard deviation (SD) as a summary statistic of the variation of the data, and standard error (SE) as a measure of the precision of the means (Sokal and Rohlf 1969).

Results

Foraging patterns

Lions searched for prey, hunted, and fed primarily at night (Fig. 3). During the daylight hours they rested and slept in the shade of trees and low shrubs. Most of the 920 observed hunts (98%) occurred at night, during which time the frequency of hunts was 0.64/h (SD = 0.7; SE = 0.05; range 0–4). More hunts were observed between 21:30 and 22:30 ($\bar{x}$ = 1.1/h; n = 111) than during any other 1-h period. On average, lions travelled 13.2 km per 24-h day (n = 76; SD = 4.9; SE = 0.56; range 0–29.6 km).

Lions live in fission–fusion social units (Schaller 1972; Bertram 1978; Packer *et al.* 1990) and prides forage in subgroups of varying sizes. Etosha lions foraged in relatively

small groups ($\bar{x}$ = 5.6, SD = 3.8, SE = 0.12, range 1–15), when all age and sex classes were combined. Not all lions present in a group participated in the observed hunts. Adult females and subadult females regularly participated in all hunts observed (Table 1). At the age of 14 months, large female cubs sometimes took part in hunts, and by the age of 18 months they always hunted. When present in hunting groups adult males and subadult males rarely participated in hunts, and large male cubs and small cubs of both sexes never participated.

On the short-grass plains of Etosha, encounters between lions and most prey were easy to observe. Prey density was low and lions encountered prey, on average, once every 2 km (SD = 1.5, SE = 0.04, range 0–3.1/km, n = 1443 km). They hunted most of the potential prey animals encountered (Table 2), ignoring only 7% of the 913 observed prey. Springbok were the most numerous species and the most often hunted. Potential prey were ignored only when a different prey species or a different group of the same species was hunted instead, or during clashes between prides.

Prey preference was measured on 82 occasions when lions encountered two groups of different prey species (Table 3). It was rarely possible to determine the size of herds, and the species were treated as two units, irrespective of the number of individuals in each group. Large prey animals (zebra, wildebeest, and gemsbok) were generally hunted in preference to herds of springbok. But when springbok neonates were visible, they were preferred to adult springbok and, on two occasions, to large prey. Lions appeared to show no preference between zebra and wildebeest.

Lions interacted with 9 species of predators, resulting in a range of responses (Table 4). They either ignored or stalked and chased most of these species, both at feeding sites and in situations unrelated to food. Spotted hyaenas provoked the largest range of responses. On two occasions, lions killed black-backed jackals but did not feed on them.

Hunting techniques

Coordinated group hunts (classes B and C) were the most common (71%) for all prey species combined (Table 5). Lions used class C hunts significantly more often when hunting zebra and wildebeest than when hunting springbok (χ^2 = 19.16, df = 4, $P < 0.001$). There was no difference between their techniques for hunting zebra and wildebeest (χ^2 = 5.47, df = 2, ns). Lionesses cooperated more often when hunting springbok than when hunting springhare (*Pedetes capensis*) (χ^2 = 47.45, df = 2, $P < 0.001$), as only solitary lionesses hunted springhare.

The duration of hunts, classified according to the stalking patterns of lions, averaged 3.5 min (SD = 3.7, SE = 0.27, n = 185, 1–20 min) for class A hunts, 9 min (SD = 6.7, SE = 0.49, n = 187, 1–40 min) for class B hunts and 14.2 min (SD = 12.1, SE = 0.81, n = 224, 1–90 min) for class C hunts. Class B hunts were of significantly longer duration than class A hunts (Mann–Whitney U-test: U = 23620, n_1 = 185, n_2 = 187, $P < 0.001$), and class C hunts were longer than class A or B (U = 31515.5, n_1 = 187, n_2 = 223, $P < 0.001$).

Hunts of springbok ($\bar{x}$ = 7.4 min, SD = 6.5, SE = 0.32, n = 406, 1–56 min) were of significantly shorter duration than those on wildebeest and zebra (U = 93446.5, n_1 = 406, n_2 = 108, $P < 0.001$), and zebra hunts ($\bar{x}$ = 14.6, SD = 10.5, SE = 1.8, n = 108, 1–60 min) were similar in duration to wildebeest hunts ($\bar{x}$ = 16.0, SD = 12.3, SE = 2.11, n = 34, 3–62 min; U = 7641.5, n_1 = 108, n_2 = 34, $P > 0.05$).

When all observations of wind direction during hunts were combined (n = 310), lions hunted upwind (n = 88) significantly more often than downwind (n = 43; binomial test, $P < 0.001$). The frequency of both crosswind (n = 179) and upwind hunts was higher than expected (χ^2 = 19.7, df = 1, $P < 0.001$). The success rates of upwind (17%) and crosswind hunts (19%) were similar (Fisher's test, ns), and these two together were more successful than downwind hunts (4%) (Fisher's test, $P < 0.001$).

TABLE 2. Prey species encountered and those hunted by lions on the plains of Etosha National Park over a foraging distance of 1443 km

	No. encountered	No. hunted	No. ignored
Springbok	677	625	52
Zebra	139	137	2
Wildebeest	58	56	2
Gemsbok	16	16	0
Giraffe (*Giraffa camelopardalis*)	6	5	1
Kori bustard (*Ardeotis kori*)	6	6	0
Black-faced impala (*Aepyceros melampus petersii*)	4	4	0
Ostrich (*Struthio camelus*)	3	3	0
Steenbok (*Raphicerus campestris*)	2	2	0
Kudu (*Tragelaphus strepsiceros*)	1	1	0
Aardvark (*Orycteropus afer*)	1	1	0
Springhare*	—	27	—
Hare (*Lepus* spp.)*	—	4	—
Korhaan (*Eupodotis* spp.)*	—	9	—
Quails*	—	5	—
Rodents*	—	6	—
Total†	913	856	57
Total no. of hunts		920	

*Rate of encounter was not measured, as species are too small.
†Excluding species for which the encounter rate was not measured.

TABLE 3. Prey preference of lions in Etosha National Park, measured by the frequency of lions choosing to hunt one prey species rather than another

Prey species encountered	n	Prey species most often hunted	n	Binomial test
Springbok vs. zebra	24	Zebra	21	$P < 0.001$
Springbok vs. wildebeest	11	Wildebeest	9	$P < 0.03$
Springbok vs. gemsbok	4	Gemsbok	4	$P < 0.001$
Zebra vs. wildebeest	11	Zebra	6	ns
Springbok vs. springbok lamb	29	Springbok lamb	29	$P < 0.001$
Gemsbok vs. springbok lamb	1	Springbok lamb	1	—
Ostrich vs. springbok lamb	1	Springbok lamb	1	—
Gemsbok vs. gemsbok calf	1	Gemsbok calf	1	—

TABLE 4. An analysis of the outcome of interactions between lions and other predators in Etosha National Park during 3134 h of observations

Predator	*n*	Stalk/ chase	Ignore	Avoid	Disturbed by	Kill	Scavenge from	Lose kill to
Spotted hyaena	21	6	2	1	8	0	3	1
Jackal (*Canis mesomelas*)	17*	13	—*	0	0	2	2	0
Aardwolf (*Proteles cristatus*)	12	4	8	0	0	0	0	0
Cape fox (*Vulpes chama*)	9	3	6	0	0	0	0	0
African wild cat (*Felix lybica*)	9	1	8	0	0	0	0	0
Honey badger (*Mellivora capensis*)	2	2	0	0	0	0	0	0
Cheetah (*Acinonyx jubatus*)	2	1	0	0	0	0	1	0
Brown hyaena (*Hyaena brunnea*)	1	1	0	0	0	0	0	0
Bat-eared fox (*Otocyon megalotis*)	1	1	0	0	0	0	0	0

*As jackals were present at all feeding sites and regularly elsewhere, the number of times lions encountered and ignored jackals was not recorded.

TABLE 5. Classification of 795 of the observed hunts on different prey species by lions in Etosha National Park

	Class A	Class B	Class C	Total
Springbok	153	167	209	529
Zebra	23	49	61	133
Wildebeest	6	11	32	49
Gemsbok	0	2	11	13
Springhare	23	1	0	24
Other large species*	4	2	3	9
Other small species†	24	9	5	38
Total	233	241	321	795

NOTE: Class A represents solo and noncoordinated group hunts, whereas classes B and C depict two escalating levels of coordinated cooperative hunts (see Methods for definitions).

*Includes giraffe, kudu, and ostrich.

†Includes quails, rodents, steenbok, hare, korhaan, kori bustard, and aardvark.

TABLE 6. Hunting success of lions in Etosha National Park on different prey species

Prey species	No. of hunts observed	No. of successful hunts	Success rate (%)
Springbok	625	81	13
Zebra	136	15	11
Wildebeest	56	17	30
Gemsbok	16	4	25
Springhare	27	14	52
Total small prey (<50 kg)	703	99	14
Total large prey (>50 kg)	217	38	18
Total	920	137	15

Hunting success

Lions on the plains of Etosha averaged one kill for every 6.7 hunts, a success rate of 15% (Table 6). Capture success rates varied among different prey species, zebra being the least vulnerable, followed closely by springbok, and wildebeest being the most vulnerable among the commonly encountered ungulates.

For all prey species, lions were more successful during class C hunts (27% success rate) than during class A (14%) and class B hunts (4%). Class C hunts contributed to 68% of the kills, class B to 6%, and class A to 26% ($n = 126$). The partially coordinated group hunts (class B) were surprisingly less successful than class A hunts; however, more than 90% ($n = 33$) of the kills resulting from class A hunts were of small and vulnerable prey such as neonates, springhare, and kori bustards. Class C hunts of springbok were more successful (27%) than class B (3%) and class A hunts (10%). Again, 86% of the class A kills ($n = 15$) were of springbok lambs. The same was true for large prey (zebra, wildebeest, and gemsbok), where the success rate was 26% for class C, 0% for class B, and 14% for class A hunts, and all the class A kills were of neonates. Class C hunts constituted 73% of all the springbok kills and 87% of all the large-prey kills.

Lions tended to be more successful in large groups (Fig. 4) when hunting all prey species, zebra, and wildebeest. Solitary lionesses were the only group size to regularly hunt springhare. When this prey species and vulnerable neonates of springbok and wildebeest (which are available for a short time only during the wet season) are excluded, single lionesses had a low hunting success, 2.3% ($n = 43$). Because of low sample sizes, groups of 4 and 5 were combined with groups of 6 and 7. Hunting success on springbok, however, was strongly correlated with the number of hunting lionesses present (Fig. 4*d*). And most multiple kills of springbok, wildebeest, and ostrich were by larger groups (10 of the 15 observed multiple kills were by groups of 5–7 lionesses).

On 95 out of the 145 nights (66%) during which lions were followed they were successful, killing a total of 156 animals ($\bar{x} = 1.64$ animals per night; range 1–7). Ninety-six springbok were killed on 57 nights, a rate of 1.68 per night (range 1–7). Multiple kills of all prey were observed during 15 class C hunts (11% of all 137 successful hunts). Two animals were captured during a single hunt on 12 occasions, and three on 3 occasions. Multiple kills ($n = 33$) contributed to 21% of the 156 animals captured.

Lions killed 95% ($n = 164$) of the prey with which they made physical contact. Adult and subadult zebra escaped on 7 separate occasions after a lioness jumped onto them ($n = 14$), and they suffered noticeable injuries from the lioness's front claws. Once a springbok escaped after a lioness swatted it. During a mass capture of 475 zebra by Ministry of Wildlife, Conservation and Tourism officials on the plains of Etosha (Stander *et al.* 1990), 43 adults and 3 subadults were found to have scars similar to those inflicted by lions.

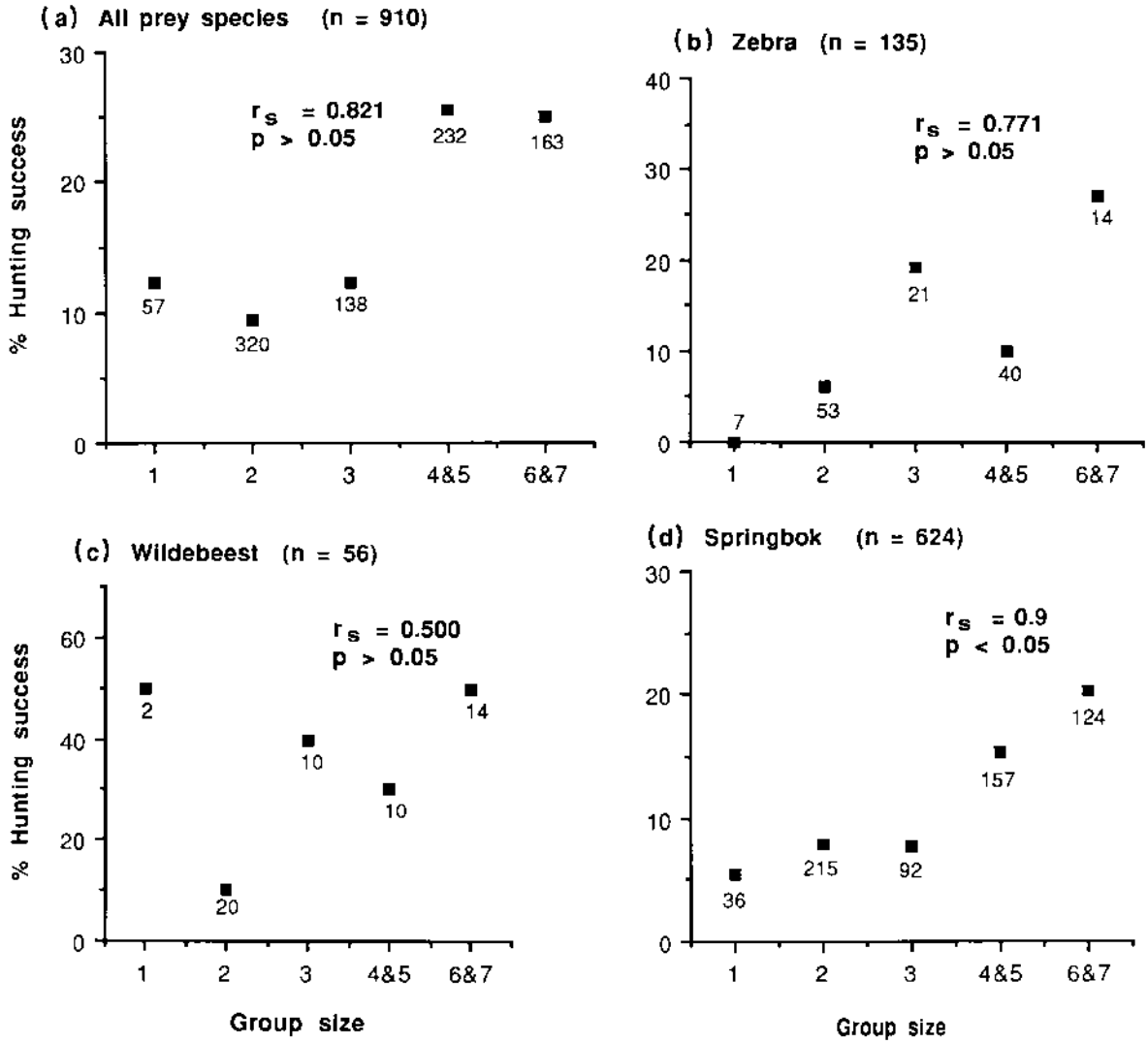

FIG. 4. Relationship between the hunting group sizes of lionesses and hunting success on all prey species combined (*a*), zebra (*b*), wildebeest (*c*), and springbok (*d*) on the plains of Etosha National Park.

Predation and feeding

Lions killed 9 different prey species (Table 7). Springbok formed the most important part of their diet, in terms of both numbers killed and estimated biomass consumed. Wildebeest were the second highest contributor, followed by zebra. Small prey (<50 kg, which included springbok and large ungulate neonates) comprised 73% of the kills and 50% of the estimated biomass. The park's mortality records (Table 8), however, indicated that zebra and wildebeest were the main prey, and Berry's (1981) study indicated zebra. Both data sets included 11% small (<50 kg) herbivores.

Adult male springbok were killed significantly more often than adult females when compared with the male:female ratio in the population (Table 9). The ratio of adult female springbok to yearlings and lambs killed by lions was similar to that of the population (personal observation). Zebra foals were more vulnerable to lion predation than adult females. Lions killed 5 adult female zebra but no males from a population of 0.4 males per female. The ratio of adult females to yearling zebra in the kill sample was similar to that of the population. Among wildebeest, lions appeared to kill more adult males, yearlings, and calves than they did adult females when related to the ratios found in the population by Berry (1980).

Lions in Etosha killed most of their food. They were observed to scavenge from 3 anthrax-infested carcases and took the kills of spotted hyaenas three times, black-backed jackal twice, and cheetah once. In total, 9 food items, or an estimated 376 kg biomass, resulted from scavenging, contributing to only 5.5% of the food items and 5.6% of the estimated biomass consumed.

The feeding times of lions on carcases in 3 different size categories varied markedly (Table 10). Very small carcases were mostly eaten by single lions and were therefore not affected by lion group size at the kill ($r_s = -0.04$, $t = -0.13$, $n = 11$, ns). The feeding times on small and medium-sized carcases decreased significantly with increase in lion group size; this was true for both the time to ripping apart ($r_s = 0.54$, $t = 3.46$, $n = 31$, $p < 0.01$) and feeding time ($r_s = -0.61$, $t = -4.51$, $n = 31$, $P < 0.001$). Springbok were ripped apart in an average of 7.6 min (SD = 10.7, SE = 1.94, $n = 30$, range 1–41) and consumed in 42 min (SD = 54.9, SE = 9.56, $n = 33$, range 2–255). Among large carcases there was no correlation between feeding time and number of lions present ($\tau = 0.165$, $z = 0.825$, $n = 14$, ns). At all carcases <80 kg, few remains were found after the

TABLE 7. Analysis of numbers of prey killed and estimated biomass consumed by lions on the plains of the Etosha National Park

	No. of kills*	Edible biomass† (kg)
Springbok	96 (62)	2317 (37)
Adult male	29 (19)	1044 (16)
Adult female	18 (12)	567 (9)
Subadult male	9 (6)	239 (4)
Subadult female	3 (2)	72 (1)
Yearling	13 (8)	270 (4)
Lamb	24 (15)	125 (2)
Wildebeest	20 (12)	1802 (28)
Adult male	1 (1)	134 (2)
Adult female	5 (3)	603 (10)
Subadult male	5 (3)	503 (8)
Yearling	4 (3)	338 (5)
Calf	5 (3)	225 (4)
Zebra	15 (9)	1526 (24)
Adult female	5 (3)	1005 (16)
Yearling	2 (1)	161 (3)
Foal	8 (5)	360 (6)
Springhare (adult)	14 (9)	42 (1)
Gemsbok	4 (3)	342 (5)
Adult female	2 (1)	241 (4)
Yearling	2 (1)	101 (2)
Kori bustard	3 (2)	15 (0.2)
Ostrich	2 (1)	134 (2)
Kudu	1 (1)	121 (2)
Aardvark	1 (1)	45 (1)
Total	156	6244

*Numbers in parentheses show percentage of total kills.
†Calculated by subtracting the estimated percent wastage (Mills 1990) from the average mass for each carcase. Numbers in parentheses show percentages of total edible biomass.

TABLE 8. Comparisons between lion kills (percentages) derived from direct and fortuitous observations in Etosha National Park

	Direct observations; this study (n = 156)	Fortuitous observations: Mortality records* (n = 72)	Fortuitous observations: Berry 1981 (n = 110)
Springbok	62	11	11
Zebra	9	33	61
Wildebeest	12	24	19
Gemsbok	3	11	8
Springhare	9	0	0
Ostrich	1	0	1
Kori bustard	2	0	0
Kudu	1	7	0
Aardvark	1	0	0
Giraffe	0	14	0

*Records based on carcase assessments of prey killed by lions for the same period and immediate area as in the present study (Etosha Ecological Institute, unpublished data).

lions had left the area, despite an effort to locate skulls and lower jaws of the prey.

Capture techniques

Direct observations (n = 143) of lions capturing prey, though not corrected for possible individual variation, revealed descriptive evidence of cooperation and specialization. Lions

TABLE 9. Age and sex ratios of prey animals in the population versus ratios of those killed by lions in Etosha National Park

Age and sex ratio*	Population	Lion kills	χ^2†
Springbok			
A ♀ : A ♂	1:0.75 (n=1993)	1:1.81 (n=59)	10.68 $P < 0.01$
A ♀ : yearling	1:0.58 (n=1795)	1:0.72 (n=34)	0.20 $P > 0.05$
A ♀ : lamb	1:0.59 (n=1862)	1:1.14 (n=45)	2.77 $P > 0.05$
Zebra			
A ♀ : A ♂	1:0.36 (n=303)	1:0 (n=5)	1.81 $P > 0.05$
A ♀ : yearling	1:0.44 (n=320)	1:0.4 (n=7)	0.01 $P > 0.05$
A ♀ : foal	1:0.32 (n=295)	1:1.6 (n=13)	8.70 $P < 0.01$
Wildebeest‡			
A ♀ : A ♂	1:0.63	1:1.2 (n=11)	1.13 $P > 0.05$
A ♀ : yearling	1:0.42	1:0.8 (n=9)	0.95 $P > 0.05$
A ♀ : calf	1:0.66	1:1 (n=10)	0.44 $P > 0.05$

*A, adult.
†Population versus lion kills; df = 1.
‡Data from Berry (1980).

mostly cooperated and captured prey from an ambush position (n = 81) (binomial test, $p < 0.05$), by leaping at it, or by charging a maximum distance of 10 m. During the remaining 62 hunts, lions captured prey from the rear or side after a rush of up to 150 m. Most springbok (n = 53) were captured from the ambush position ($P < 0.001$); springbok lambs (P = 0.14), springhare ($P < 0.01$), and other small animals (P = 0.05), however, were more often captured after a rush. Large prey (<50 kg) were caught in both ambush (n = 14) and rush (n = 11) situations (P = 0.345).

The physical methods practiced by lions in capturing prey vary according to the species or size of the prey (Table 11). Adult springbok, who appeared to be much faster than lions, were most often grabbed in midair (always from an ambush position) while jumping to escape a lion. Springbok lambs were easier prey, and in most cases lions overtook lambs and either slapped them to the ground with one paw or grabbed them with their mouth or front claws. Large prey required more force and lions most often jumped on the back of the prey, causing it to fall. When attacking large prey head on, lions charged at them and collided into their forequarters, knocking them off balance and causing both to crash to the ground, the lions maintaining their grip on the prey with front claws and teeth. Springhare, with a "zigzag" fleeing pattern, were mostly outrun by lions and slapped to the ground with one paw. Capture methods for other small prey showed no pattern, as the group consisted of a variety of species with different fleeing patterns. A single lioness was observed to be fully capable of subduing all prey species captured.

Food consumption

During 145 days, groups of lions totalling 981 (most seen more than once) were observed to feed on 165 food items, consuming an estimated biomass of 6719 kg. Each hunting lioness acquired an estimated average of 10.3 kg/day (SD =

TABLE 10. Average, variance, and range of feeding times of lions on very small (<5 kg), small–medium (5–80 kg), and large (>80 kg) carcases

	Carcase ripped apart*	Carcase consumed†		
	Small–medium (min)	Very small (min)	Small–medium (min)	Large (h:min)
Mean	7.4	25.5	45.5	6:23
SD	10.5	16.7	61.7	5:45
SE	1.9	10.2	10.2	92:2
Range	1–14	2–60	2–255	0:21–24:00
n	31	11	37	14

*Feeding time was measured from the time of capture to the point at which the carcase was ripped apart.
†Feeding time was measured from the time of capture to the end of the feeding session (when fewer than one-third of the lions might still be chewing on a bone).

TABLE 11. Methods of prey capture by lions during 135 direct observations in Etosha National Park

	Jump on	Collide over	Grab with claws	Grab in midair	Grab with mouth	Slap down	χ^2
Springbok (n=63)	—	2	17	31	—	13	27.3; df = 3 $P < 0.001$
Springbok lamb (n=22)	—	0	4	2	4	12	10.7; df = 3 $P < 0.02$
Large prey* (n=25)	17	6	2	—	—	-	14.5; df = 2 $P < 0.001$
Springhare (n=14)	—	—	0	0	1	13	10.2; df = 1 $P < 0.01$
Other small prey† (n=11)	—	3	3	2	0	3	

NOTE: Statistics are based on the null hypothesis that the frequencies of use of the capture techniques are equal.
*Including zebra, wildebeest, gemsbok, kudu, and ostrich.
†Including aardvark, kori bustard, zebra foals, and wildebeest calves.

15.2, SE = 1.24, n = 145, range 0–110.6 kg). The variation in food acquisition over time was large. For example, when a group of 9 lionesses was followed for 13 consecutive days, consumption was 2.01 kg/day per lioness (SD = 3.8, SE = 1.08, range 0–12.6 kg). In contrast, a group of 7 lionesses followed for 9 consecutive days acquired 14.43 kg/day per lioness (SD = 6.3, SE = 5.29, range 0–44.3 kg).

Food acquisition varied considerably between the dry and wet seasons. Although the distances moved by lions per day during the dry and wet seasons (U = 1992.0; n_1 = 54; n_2 = 18; $P < 0.1$) and their overall hunting success rates (14.7 and 15.2%, respectively) were similar, lions encountered significantly more prey in the wet season (8.66/night) than in the dry season (4.35/night; χ^2 = 13.3, df = 1, $P < 0.001$). Thus, the average food intake of 14.1 kg/day per lioness for the wet season (SD = 13.5, SE = 2.02, n = 45, range 0–47.7) was significantly higher than the consumption in the dry season, 8.7 kg/day per lioness (SD = 15.5, SE = 1.51, n = 106, range 0–110.6; U = 7307.5, n_1 = 106, n_2 = 45, $P < 0.01$).

Optimum group sizes for foraging

The average daily food acquisition by lionesses in groups of different sizes was analyzed separately for the dry and wet seasons. Lionesses hunted most prey they encountered and, apart from springhare, lioness group size had no effect on the prey species hunted (G-test: G = 11.4, df = 12, ns), nor were any species captured disproportionately more often by lionesses in groups of a particular size (G = 16.5, df = 12, ns). Hunting success rates for all prey species were therefore lumped together and compared with food intake.

During the dry season, lionesses in groups of 2 had the highest food intake (Fig. 5), even though their hunting success was below 10%. In contrast, the higher hunting success rate of solitary lionesses yielded a lower food intake. Hunting success rate in the dry season increased with the number of lionesses in the group ($P < 0.05$), but did not appear to be related to food intake. There were no significant differences between the daily food intake of lionesses in groups of 2, 3, 6, and 7, or even between groups of 2 and 4–5. Groups of 6 and 7 had the highest hunting success rate (34.2%), allowing a per capita payoff of 10.3 kg/day, second to groups of 2.

The hunting success rate in the wet season was not related to foraging group size (r_s = 0.179, N = 7, ns), being highest for solitary lionesses and lowest for groups of 2. Groups of 3 gained the highest per capita food intake (Fig. 6), but it was not significantly higher than that of solitary animals or groups of 2. The daily food intake for solitary animals, though similar, was highly variable and less stable than for groups of 2. Smaller foraging groups (1–3) gained higher rewards than

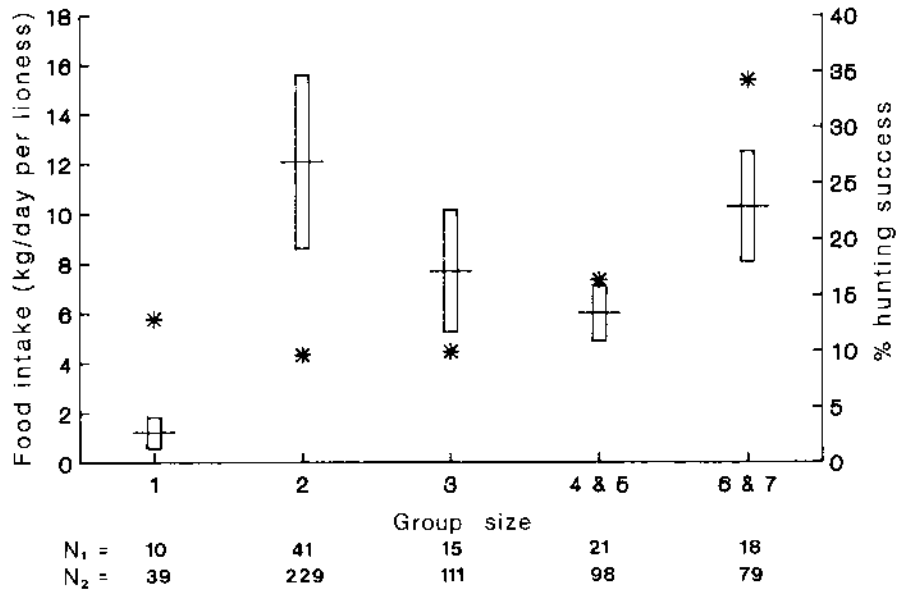

FIG. 5. Daily food intake (kg) per lioness for five group sizes in the dry season, shown as mean and standard error, with hunting success (*) for all species in each group size. N_1, number of days of observation of food intake in each group size; N_2, number of observed hunts by lionesses in each group size. Group 1 vs. group 2: $U = 1108.0$, $n_1 = 10$, $n_2 = 41$, $P < 0.05$; group 2 vs. groups 3 and 6–7: Kruskal–Wallis test: $H = 0.095$, df = 2, $n = 74$; ns; group 2 vs. group 4: $U = 1205.0$, $n_1 = 41$, $n_2 = 18$, ns; correlation of hunting success and group size: $r_s = 0.821$, $n = 7$, $P < 0.05$, one-tailed.

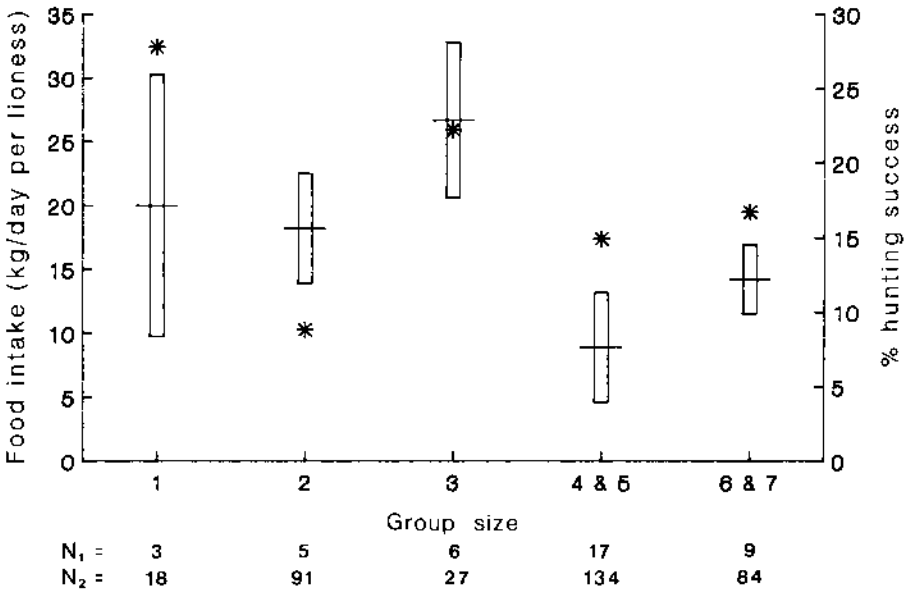

FIG. 6. Daily food intake (kg) per lioness for five group sizes in the wet season, shown as mean and standard error, with hunting success (*) for all species in each group size. N_1, number of days of observation of food intake in each group size; N_2, number of observed hunts by lionesses in each group size. Group 1 vs. groups 2 and 3: $H = 0.15$; df = 2; $n = 14$; ns; groups 1–3 vs. groups 4–7: $U = 452.5$, $n_1 = 14$, $n_2 = 31$, $P < 0.002$.

larger groups of 4–7 ($P < 0.002$). Lionesses in groups of all sizes acquired higher daily food intake in the wet season than in the dry season (Wilcoxon's matched pairs test: $T = 2$, $n = 7$; $P < 0.05$).

In the dry season, foraging grouping patterns for all pride sizes favoured pairs (Fig. 7*a*). This corresponds to the high daily food intake acquired by groups of that size, but lionesses infrequently foraged in groups of 6 or 7, which had the second highest food intake. Although prides of 6 hunted regularly in pairs, they showed no significant tendency to form groups of any particular size. During the wet season (Fig. 7*b*), when smaller groups (1–3 lionesses) gained a higher food intake, lionesses in prides of 6 often foraged in larger groups of 5 or 6, while prides of 7 often foraged in pairs and groups of 6. During both seasons lionesses in prides of all sizes infrequently hunted alone. Foraging groups were significantly smaller (2 females) during the dry season than during the wet season, for prides of both 6 (Kolmogorov–Smirnov two-sample test: $D_{max} = 0.38$; $P < 0.01$) and 7 females ($D_{max} = 0.25$; $P < 0.01$).

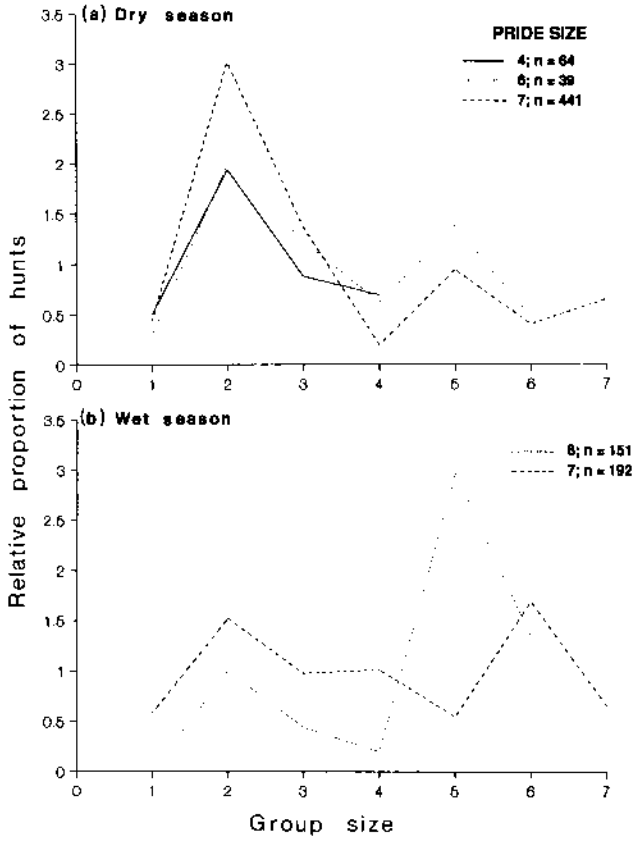

FIG. 7. Relative proportion of hunts during which lionesses (older than 18 months) were found in groups of each size during 910 observed hunts in dry (*a*) and wet seasons (*b*) in Etosha National Park. Data for similar-sized prides were combined. To avoid bias resulting from subgroup associations, the relative proportion represents the observed proportion of hunts in each group size, $y(x/n)$, where y is the observed number of hunts, x is the pride size, and n is the total number of sightings of prides of that size (Packer *et al.* 1990). Therefore, lionesses found equally often in groups of each size will have a relative frequency of 1.0. Statistical calculations are based on untransformed data, testing the null hypothesis that lionesses forage equally often in groups of each size. (*a*) Dry season: lionesses in prides of 4 and 7 showed heterogeneous grouping patterns (*G*-test; $P < 0.05$), lionesses in both prides hunting more often in pairs than expected (binomial test; $P < 0.01$). (*b*) Wet season: grouping patterns in both prides were heterogeneous (*G*-test; $P < 0.05$), lionesses in prides of 6 hunting in groups of 5 more often than expected; similarly, lionesses in prides of 7 hunted more frequently in groups of 6 ($P < 0.01$). For all pride sizes in both seasons (except prides of 6 during the dry season), lionesses hunted less often alone than expected ($P < 0.05$).

Discussion

Foraging patterns

It is well known that lions are nocturnal (Eloff 1984; Elliot *et al.* 1977; Rudnai 1979; Schaller 1972; Van Orsdol 1982*a*), although diurnal hunting is common in areas that provide sufficient vegetation cover (Van Orsdol 1984). On the plains of Etosha, with an average grass cover of 0.1 m and scattered shrubs of up to 0.3 m, lions hunted almost entirely at night. Van Orsdol (1984) recorded 0.04–0.1 hunts/h in Uganda, while lions in Etosha hunted at a higher rate of 0.64 hunts/h. This may be explained by the lower hunting success and larger distances travelled by Etosha lions ($\bar{x}$ = 13.2 km/night) as opposed to 2.2–5 km/day measured for East African lions (Wright 1960; Schaller 1972; Rudnai 1973; Van Orsdol 1984). In the southern Kalahari, an arid environment similar to Etosha, lions also travelled long distances ($\bar{x}$ = 11.8 km/day, maximum 41.2 km; Eloff 1984).

Prey preference by lions (Pienaar 1969; Rodgers 1974; Rudnai 1974; Berry 1981) has been presented as the preference rating (PR) of each prey species, where PR = kill frequency/relative abundance of prey. It is suggested that this method is rather an indication of the vulnerability of prey to lion predation, as it is likely subject to the spatial distribution of prey (Sunquist and Sunquist 1989) and to the lions' hunting success on each species. Prey preference is best estimated from direct observations. Schaller (1972) found that while preferring large prey, lions eat whatever they can catch, and kill the easiest prey (Smuts 1982). Observations in Etosha supported these concepts; lions hunted almost everything they encountered, showing a preference for large prey when opportunity permitted.

Hunting success and cooperation

The increase in duration of hunts in classes A–C reflects a hypothetically greater hunting effort by lions during hunts of a cooperative nature. Class A group hunts, which could also be viewed as simple cooperation (Packer and Ruttan 1988), resulted mainly in the capture of very small prey and neonates. Class C hunts, the major means of capturing prey, resemble coordinated cooperation, with division of labour (Stander 1992), and an apparent awareness of the probable consequences of activities (Schaller 1972; Griffin 1984). Fundamentally, class B hunts are similar to class C hunts, and the behaviour of lionesses during both resembles that of Scheel and Packer's (1991) "pursuers." However, a distinction between these two classes lies in the attack phase; during class B hunts lions charge at the prey, regardless of the positions or stalking activities of other group members. Although this outcome may occasionally be a result of the prey's behaviour, it is suggested that class B hunts reflect a less precisely coordinated group effort. Data on coordinated group hunts are presented elsewhere (Stander 1992).

Several authors found that lions do not consider wind direction when hunting (Schaller 1972; Elliot *et al.* 1977), and that it did not affect hunting success (Elliot *et al.* 1977), although Schaller (1972) observed that some hunts were more successful upwind than downwind. Etosha lions hunted upwind significantly more often than downwind and were less successful during the latter.

The overall hunting success for Etosha (15%) was low compared with that observed in other studies, where success rates ranged from 21 to 38.5% (Schaller 1972; Elliot *et al.* 1977; Eloff 1984; Van Orsdol 1984). This was probably due to hunting in open and short-grass plains (Smuts 1978; Van Orsdol 1984). An increase in hunting success with group size has not been consistently observed among lions (Schaller 1972; Elliot and Cowan 1978; Van Orsdol 1984). Schaller (1972) found an advantage only for hunting in pairs. Single lionesses in Etosha were more successful than groups of 2 (Fig. 4*a*) because they mostly hunted springhare, which were easily captured. Disregarding hunts of springhare, the hunting success for all species improved linearly with group size.

Cooperation in the hunting behaviour of the Etosha lions is reflected in the methods of capturing prey. While fleeing from

one lioness most prey were seized by another from an ambush position. Although it has been suggested that cooperative stalking by lions is coincidental (Kruuk and Turner 1967; Kruuk 1982), my observations of repeated coordinated stalking and the capture of most prey from ambush positions provide basic evidence of cooperative hunting and the benefits derived from it. Cooperation may also allow lions to subdue larger prey (Bertram 1979; Gittleman 1989) like buffalo (Packer *et al.* 1990), although single lionesses in Etosha were mostly proficient enough to overcome large prey. On seven occasions when a zebra escaped a lioness, it did so at first contact, before a second lioness could assist.

Predation and feeding

In most African conservation areas lions feed predominantly on large ungulates, and, where abundant, wildebeest, buffalo (*Syncerus caffer*), and zebra are the principal prey species (Schaller 1972; Bertram 1979; Sunquist and Sunquist 1989). Etosha lions appear to be minor predators on zebra and wildebeest, and kill mostly small animals (73% of all kills). In contrast, the park's mortality records and reports by Berry (1981) account for only 11% small animals. This discrepancy is not surprising considering that lions hunt almost entirely at night and that small and medium-sized carcases (<80 kg) are mostly consumed in less than 1 h, leaving only trace remains.

The tendency for lions to kill prey in certain age and sex segments of the populations has also been observed elsewhere. Mills (1990) found similar selection of adult male springbok in the southern Kalahari. Schaller (1972) and Rudnai (1974) likewise observed lions to kill more zebra foals than adult females in proportion to the population. Wildebeest bulls were also more vulnerable to predation than females in the Serengeti (Schaller 1972), but not at three locations in South Africa (Hirst 1969; Pienaar 1969; Mills 1990).

Lions on the plains of Etosha consumed, on average, 8.7 kg/day per lioness in the dry season and 14 kg/day per lioness in the wet season. Packer *et al.* (1990) recorded an average food intake of 8.5 kg/day per lioness during periods of prey abundance. They also suggested that females may increase their food intake during periods of prey abundance (see Katz 1974). The markedly higher per capita food intake by Etosha lions during the wet season could be explained by food deprivation in the prolonged dry season. Van Orsdol (1982*b*) found food consumption of lions in Uganda to be related to hunting success and not to prey density. Lions in Etosha, an area of lower prey density, acquired significantly more food in the wet season, when prey were more abundant.

Scavenging and interactions with other predators

On the plains of Etosha, scavenging accounted for less than 6% of both food items and estimated biomass consumed by lions. Mills (1990) also recorded Kalahari lions as scavenging only 4.6% of food items, while Serengeti lions were recorded as scavenging 16–33% (Schaller 1972) and >40% (Packer *et al.* 1990) of food items.

Interspecific competition between lions and spotted hyaenas may be considerable, as they generally prey on the same species (Kruuk 1972; Schaller 1972; Mills 1990). Clashes over food between the two species were rare in Etosha and in the southern Kalahari (Mills 1990). East African lions obtained 42–81% of their scavenged meat from, and lost 44% of their kills to, spotted hyaenas (Kruuk 1972; Schaller 1972). Packer (1986), however, showed that these estimates of scavenging by hyaenas were too high, and recorded only negligible amounts of meat lost to hyaenas (Packer *et al.* 1990). In Etosha, interactions between lions and spotted hyaenas, which mostly favoured the former, were generally rare, probably as a result of the low densities.

Lions either ignored or stalked and chased other predators. They were observed to behave aggressively towards jackals and even to kill them. In contrast, lions paid little attention to jackals elsewhere (Schaller 1972; Eloff 1984), although in the Skeleton Coast, Namibia, lions often captured and ate jackals (S. Braine, personal communication, 1986).

Optimum foraging group sizes

Etosha lionesses always participated in hunts, in contrast to those in the Serengeti, an area of higher prey and lion biomass (East 1984), where the probability of females "refraining" from hunting was 0.33 (Scheel and Packer 1991). Adult males, however, behaved similarly to those in the Serengeti and were generally nonparticipants in hunts.

Foraging group patterns among lions have provoked considerable debate. Gittleman (1989) suggested that group size is linked to food acquisition, whereas Van Orsdol (1982*b*) and Packer *et al.* (1990) found no correlation between group size and food supply or pride size. It has also been suggested that prey size determines lion group size (Kruuk and Turner 1967; Kleiman and Eisenberg 1973; Caraco and Wolf 1975). Several authors have discussed the relationship between lion group size and foraging success (Caraco and Wolf 1975; Lamprecht 1978; Rodman 1981; Clark 1987; Giraldeau and Gills 1988), using mostly Schaller's (1972) data. However, Packer *et al.* (1990) showed that Schaller's data are inappropriate for such analysis and provided new data from the Serengeti to show that foraging success does not account for grouping preferences.

During the dry season in Etosha, only solitary hunters did not meet the estimated minimum daily requirement of 5–8.5 kg/day (Packer *et al.* 1990). Group hunting therefore appeared to be essential. Lionesses in groups of 2 obtained the highest food intake, and also foraged most often in groups of this size. They rarely hunted in groups of 6 or 7, which showed a high daily food intake. These results differ from those obtained in the Serengeti (Packer *et al.* 1990), where lions foraged primarily on warthog (*Phacochoerus aethiopicus*) and buffalo, and groups of 1 and 5–7 acquired the highest daily food intake in the lean season but rarely foraged in groups of these sizes. With aggression at small carcases often leading to fragmentation of large groups (Van Orsdol *et al.* 1985), Etosha lions, with an abundance of carcases <50 kg in their diet, foraged in pairs, the optimum foraging group size.

During the wet season in Etosha, lionesses in groups of all sizes met the estimated minimum daily requirement (Packer *et al.* 1990). This is probably due to the higher density of prey and the abundance of neonates. Although lionesses gained a higher per capita food intake in small groups (1–3), lionesses in prides of 6 foraged in larger group sizes, whereas prides of 7 showed a tendency to forage in both large and smaller groups. When prey were abundant in the Serengeti (Packer *et al.* 1990), lion group size did not affect food intake and, except for solitary lionesses, who were often found alone, their grouping patterns did not differ from those in periods of prey scarcity. Grouping patterns in Etosha during the wet season are possibly related to other factors such as the defence

of young, carcases, and territories (Schaller 1972; Bertram 1978; Packer 1986; Packer *et al.* 1990).

Population declines

In the light of recent improvements in methods, two comments about Berry's (1981) findings are appropriate. First, assessments of lion predation may have overestimated the density of large prey species. Secondly, because few lions were marked, estimates of lion density may have been inflated. Nevertheless, such large differences could not be due to methodological problems alone.

With wildebeest, at high density, outnumbering springbok, lions may have been responsible for the decline in the former species, based on the high hunting success on it. Zebra, however, are difficult to capture on the open plains and it is doubtful whether lions, even under high-density conditions, could be major predators. The apparent decrease in numbers of lions during the 1980s may have been related to the relative increase in numbers of springbok, for the following reasons: hunting success on springbok was low, and though it increased with hunting group size, it provided lions with small carcases which were, on average, consumed in 42 min. Feeding on small carcases by large groups caused aggression that resulted in the splitting of subgroups (Schaller 1972; Van Orsdol 1982*a*; Van Orsdol *et al.* 1985). Low success rate and small meal size required lions to constantly move long distances at night, resulting in high cub mortality rates (Schaller 1972; Bertram 1973; Van Orsdol 1982*b*; Eloff 1984; Van Orsdol *et al.* 1985).

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Berry, H. H. 1980. Behavioural and eco-physiological studies on the blue wildebeest (*Connochaetes taurinus*) at the Etosha National Park. Ph.D. thesis, University of Cape Town, South Africa.

Berry, H. H. 1981. Abnormal levels of disease and predation as limiting factors for wildebeest in the Etosha National Park. Madoqua, **11**: 242–253.

Bertram, B. C. R. 1973. Lion population regulation. East Afr. Wildl. J. **11**: 215–225.

Bertram, B. C. R. 1978. Living in groups: predators and prey. *In* Behavioural ecology: an evolutionary approach. *Edited by* J. R. Krebs, and N. B. Davies. Sinauer, Sunderland, MA. pp. 64–96.

Bertram, B. C. R. 1979. Serengeti predators and their social systems. *In* Serengeti: dynamics of an ecosystem. *Edited by* A. R. E. Sinclair, and M. Norton-Griffiths. The University of Chicago Press, Chicago. pp. 221–248.

Caraco, T., and Wolf, L. L. 1975. Ecological determinants of group sizes of foraging lions. Am. Nat. **109**: 343–352.

Clark, C. W. 1987. The lazy, adaptable lions: a Markovian model of group foraging. Anim. Behav. **35**: 361–368.

East, R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr. J. Ecol. **22**: 245–270.

Elliot, J. P., and Cowan, I. McT. 1978. Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. Can. J. Zool. **56**: 1726–1734.

Elliot, J. P., Cowan, I. McT., and Holling, C. S. 1977. Prey capture by the African lion. Can. J. Zool. **55**: 1811–1828.

Eloff, F. C. 1984. Food ecology of the Kalahari lion *Panthera leo*. Koedoe, **27**(Suppl.): 249–258.

Gasaway, W. C., Mossestad, K. T., and Stander, P. E. 1989. Demography of spotted hyaenas in an arid savanna, Etosha National Park, South West Africa/Namibia. Madoqua, **16**: 121–127.

Gasaway, W. C., Mossestad, K. T., and Stander, P. E. 1991. Food acquisition by spotted hyaenas in Etosha National Park, Namibia: predation versus scavenging. Afr. J. Ecol. 1991. **29**: 64–75.

Giraldeau, L., and Gills, D. 1988. Do lions hunt in group sizes that maximize hunters' daily food returns. Anim. Behav. **36**: 611–613.

Gittleman, J. L. 1989. Carnivore group living: comparative trends. *In* Carnivore behavior, ecology and evolution. *Edited by* J. L. Gittleman. Cornell University Press, Ithaca, N.Y. pp. 183–207.

Griffin, D. R. 1984. Animal thinking. Harvard University Press, Cambridge, Mass.

Hirst, S. M. 1969. Predation as a regulating factor of wild ungulates in a Transvaal lowveld nature reserve. Zool. Afr. **4**: 199–230.

Katz, P. L. 1974. A long-term approach to foraging optimization. Am. Nat. **108**: 758–782.

Kruuk, H. 1972. The spotted hyaena. The University of Chicago Press, Chicago.

Kruuk, H. 1982. Interactions between Felidae and their prey species: a review. *In* Cats of the world: biology, conservation and management. *Edited by* S. D. Miller and D. D. Everet. National Wildlife Federation, Washington, D.C. pp. 353–374.

Kruuk, H., and Turner, M. 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia, **31**: 1–27.

Kleiman, D. G., and Eisenberg, J. F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. **21**: 637–659.

Lamprecht, J. 1978. The relationship between food competition and foraging group size in some larger carnivores: a hypothesis. Z. Tierpsychol. **46**: 337–343.

Le Roux, C. J. G., Grunow, J. O., Morris, J. W., Bredenkamp, G. J., and Scheepers, J. C. 1988. A classification of the vegetation of the Etosha National Park. S. Afr. J. Bot. **54**: 1–10.

Mills, M. G. L. 1990. Kalahari hyaenas: comparative behavioural ecology of two species. Unwin Hyman, Ltd., London.

Orford, H. J. L., Perrin, M. R., and Berry, H. H. 1988. Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). J. Zool. (Lond.), **216**: 717–733.

Packer, C. 1986. The ecology of sociality in felids. *In* Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton, N.J. pp. 429–451.

Packer, C., and Pusey, A. E. 1985. Asymmetric contests in social mammals: respect, manipulation and age-specific aspects. *In* Evolution: essays in honour of John Maynard Smith. *Edited by* P. H. Harvey and M. Slatkin. Cambridge University Press, Cambridge. pp. 173–186.

Packer, C., and Ruttan, L. 1988. The evolution of cooperative hunting. Am. Nat. **132**: 159–168.

Packer, C., Scheel, D., and Pusey, A. E. 1990. Why lions form groups: food is not enough. Am. Nat. **136**: 1–19.

Pienaar, U. de V. 1969. Predator–prey relationships amongst the larger mammals of the Kruger National Park. Koedoe, **12**: 108–176.

Rodgers, W. A. 1974. The lion (*Panthera leo*, Linn.) population of the eastern Selous Game Reserve. East Afr. Wildl. J. **12**: 313–317.

Rodman, P. S. 1981. Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. Am. Nat. **118**: 275–283.

Rudnai, J. A. 1973. The social life of the lion. MTP Press, Ltd. Lancaster.

Rudnai, J. A. 1974. The pattern of lion predation in Nairobi Park. East Afr. Wildl. J. **12**: 213–225.

Rudnai, J. A. 1979. Activity rhythm of a free-ranging lion population. Carnivore (Seattle), **2**: 77–81.

Schaller, G. B. 1972. The Serengeti lion. University of Chicago Press, Chicago.

Scheel, D., and Packer, C. 1991. Group hunting behaviour of lions: a search for cooperation. Anim. Behav. **41**: 697–709.

Siegel, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.

Smithers, R. H. N. 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria, South Africa.

Smuts, G. L. 1978. Interrelations between predators, prey, and their environment. BioScience, **28**: 316–320.

Smuts, G. L. 1982. Lion. Macmillan, Johannesburg.

Sokal, R. R., and Rohlf, F. J. 1969. Biometry. W. H. Freeman and Company, San Francisco.

Stander, P. E. 1991. Demography of lions in the Etosha National Park. Madoqua, **18**(1): 1–9.

Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. Behav. Ecol. Sociobiol. **29**: 445–454.

Stander, P. E., and Morkel, P. vdB. 1991. Field immobilization of lions using disassociative anaesthetics in combination with sedatives. Afr. J. Ecol. 1991. **29**: 138–148.

Stander, P. E., and Stander, J. 1988. Characteristics of lion roars in Etosha National Park. Madoqua, **15**: 315–318.

Stander, P. E., Nott, T. B., Lindeque, P. M., and Lindeque, M. 1990. Mass marking of zebras in the Etosha National Park, Namibia. Madoqua, **17**: 47–49.

Sunquist, M. E., and Sunquist, F. C. 1989. Ecological constraints on predation by large felids. *In* Carnivore behavior, ecology and evolution. *Edited by* J. L. Gittleman. Cornell University Press, Ithaca, N.Y. pp. 283–301.

Van Orsdol, K. G. 1982*a*. Ranges and food habits of lions in Rwenzori National Park, Uganda. Symp. Zool. Soc. Lond. **49**: 325–340.

Van Orsdol, K. G. 1982*b*. Feeding behavior and food intake of lions in Rwenzori National Park, Uganda. *In* Cats of the world: biology, conservation and management. *Edited by* S. D. Miller and D. D. Everet. National Wildlife Federation, Washington, D.C. pp. 377–388.

Van Orsdol, K. G. 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. Afr. J. Ecol. **22**: 79–99.

Van Orsdol, K. G., Hanby, J. P., and Bygott, J. D. 1985. Ecological correlates of lion social organization (*Panthera leo*). J. Zool. (Lond.), **206**: 97–112.

Van Wyk, T. C., and Berry, H. H. 1986. Tolazoline as an antagonist in free-living lions immobilized with a ketamine–xylazine combination. J. S. Afr. Vet. Assoc. **57**: 99–104.

Wright, B. S. 1960. Predation on big game in East Africa. J. Wildl. Manage. **24**: 1–15.