Behav Ecol Sociobiol (1992) 29:445–454

Behavioral Ecology and Sociobiology

Cooperative hunting in lions: the role of the individual

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Received March 27, 1991/Accepted October 5, 1991

Summary. Individually identified lions (*Panthera leo*) were observed on the open, semi-arid plains in Namibia. Data from 486 coordinated group hunts were analysed to assess cooperation and individual variation in hunting tactics. Group hunts generally involved a formation whereby some lionesses ("wings") circled prey while others ("centres") waited for prey to move towards them. Those lionesses that occupied "wing" stalking roles frequently initiated an attack on the prey, while lionesses in "centre" roles moved relatively small distances and most often captured prey in flight from other lionesses. Each lioness in a given pride repeatedly occupied the same position in a hunting formation. Hunts where most lionesses present occupied their preferred positions had a high probability of success. Individual hunting behaviour was not inflexible, however, but varied according to different group compositions and to variations in the behaviour of other individuals present. The role of cooperative hunting and its apparent advantages within the semi-arid environment of Etosha National Park, Namibia, are discussed.

Introduction

Cooperative hunting aids social carnivores in securing prey in open habitats (Wilson 1975) and in three-dimensional habitats (Norris and Schilt 1988). Group hunting by terrestrial carnivores such as the lion (*Panthera leo*) is thought to reduce problems of locating and subduing large prey (Bertram 1979; Lamprecht 1981; Packer 1986), and to improve kill efficiency (Schaller 1972; Caraco and Wolf 1975). Packer (1986), however, suggests that group foraging does not exhibit conclusive advantages for lions and furthermore presents evidence (Packer et al. 1990) that foraging success does not explain the grouping patterns of female lions. They attribute grouping patterns to other factors, such as the defence of young and the maintenance of long term territories (Packer et al. 1990).

Schaller's (1972) observations of 274 group hunts provided evidence that not all lions present in the group participated in group hunts, lending support to the theoretical concept of "cheating" (Maynard Smith 1982; Packer and Ruttan 1988). Packer and Ruttan (1988), using game theoretical models, weighed the costs and benefits of cooperative hunting and showed that cooperation was not advantageous when lions captured a single prey animal per hunt, and that some individuals in larger group sizes may "cheat" (exploit the foraging activities of conspecifics) during cooperative hunts. They also showed that animals should be more cooperative when the hunting success of a solitary hunter is low. Scheel and Packer (1991) presented new data on communal hunting in the Serengeti, revealing that cooperation is common during hunts on larger and more difficult prey and that cheating is more common during communal hunts where the success rate of solitaries is high.

Lions in the semi-arid environment of Etosha National Park, Namibia, occur at low densities (2.8 lions 100 km^{-2}; Stander 1991), and live in fission-fusion social groups with no social hierarchy among pride lionesses (Schaller 1972; Packer and Pusey 1982, 1985), similar to those seen in other studies in Africa. Lionesses (2 years and older) do almost all of the hunting in mixed groups (Schaller 1972; Scheel and Packer 1991) although males may hunt on their own (Schaller 1972). Previous work in Etosha N.P. has shown that lionesses rarely scavenged, and hunted, on average, in groups of 3.6 (Stander 1992). Most hunts involved coordinated stalking by groups and are defined as cooperative hunts, analogous to Scheel and Packer's (1991) "pursuers". Hunts by solitaries were infrequent (1%) and had a low success rate (2.3%). Based on Packer and Ruttan's (1988) models, one would therefore expect Etosha lions to be more cooperative, and less likely to "cheat" than elsewhere (Scheel and Packer 1991). In this paper I examine only cooperative group hunts to consider the value of group hunting under semi-arid conditions, and to emphasize

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individual specialization as an aspect of lions' cooperative hunting strategy.

Methods

Between May 1984 and July 1988 four prides were observed for 52 observation periods, each of which lasted from 1 (24 h) to 15 days. These prides inhabited the short grass plains of Etosha N.P. (Le Roux et al. 1988). Most lions (83%; $n = 48$) were permanently marked with an individually recognizable hot brand (Orford et al. 1988). Brand marks, approximately 7 × 7 cm in size, were placed either on a foreleg or a hind limb of each lion. With night-viewing equipment these brandmarks were visible up to roughly 50 m. One to three lionesses of each pride were radio-collared. During standard immobilizations (Van Wyk and Berry 1986; Stander and Morkel 1991) lions were marked, collared and aged by the extent of tooth eruption, wear and discolouration (Smuts et al. 1978). Two unmarked lionesses were individually recognizable from natural scars. All lions were allocated into age classes described by Schaller (1972) and Smuts et al. (1978). Radio-collared lionesses were located using ground and aerial radio-telemetry.

When analysing hunting behaviour, caution was exercised in defining a hunt (Mech 1970; Kruuk 1972; Schaller 1972; Mills 1990). Two or more lionesses were considered to be hunting "cooperatively" when all lionesses stared at prey with an alert posture and facial expression (Schaller 1972) and some or all individuals subsequently stalked the prey. Some individuals stalked directly towards the prey or remained stationary, while others took an indirect route or even encircled prey. Only hunts that met these criteria ($n = 486$) were considered for the following analysis. Hunts by solitaries and those by groups where all individuals stalked directly at prey ($n = 233$) are similar to Scheel and Packer's (1991) "conformists", and were less successful (14%) than cooperative hunts (27%), and the latter contributed to 68% of the observed kills (Stander 1992).

Since the lions hunted mostly on the plains, and almost exclusively at night (Stander 1992), they were viewed from a vehicle at distances of 20–100 m with the aid of image intensifying night-glasses or a 75-W red-filtered spotlight and low-light binoculars, or with an infra-red 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 however taken not to disturb the animals or dazzle the prey when the red-filtered light was used.

Lions hunted 16 species, of which three (springbok *Antidorcas marsupialis*, zebra (*Equus burchelli* and wildebeest *Connochaetes taurinus*) contributed 83% of the prey animals killed ($n = 156$) and 89% of the biomass consumed ($n = 6244$ kg) (Stander 1992). The analysis of cooperative hunts was based on these three species, plus 28 hunts on gemsbok (*Oryx gazella*), giraffe (*Giraffa camelopardalis*) and ostrich (*Struthio camelus*). Together these are referred to as "large and fleet-footed prey".

Definitions and stalking roles. During standard observations of cooperative hunting, much attention was given to the individuals in the hunting group, with emphasis on their positions and movements in relation to other members of the group and to the prey. A "group" was defined as individuals of the same pride who were within 200 m of each other (Packer et al. 1990). "Initiating an attack" occurred when the first lioness charged at prey during a hunt and "participation" occurred when a lioness joined in on a chase initiated by another lioness. "Ambush" was defined as a crouching position from which a lioness could catch prey fleeing from another lioness, and a "rush" was when a lioness initiated an attack and captured prey after a chase of up to 150 m. Data were recorded by tape recorder and/or video. Rough diagrams were also drawn during and shortly after hunts, indicating the movements of individual lions and of the prey.

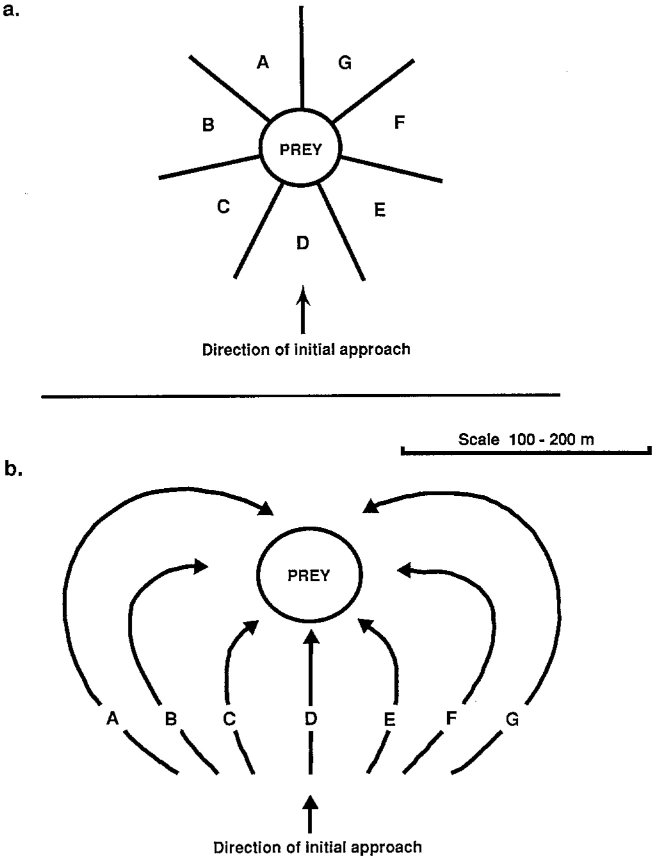

Fig. 1 a, b. Schematic diagram of seven typical stalking roles occupied by lionesses during cooperative hunts. **a** The final positions, in relation to the prey and the observer's position, occupied by lionesses in the different stalking roles. Lionesses then either charged the prey or the prey fled. These positions correspond with the typical stalking routes illustrated in Fig. 1b, and indicate "left wing" (*A–B*), "centre" (*C–E*) and "right wing" (*F–G*) stalk-categories. **b** The most typical stalking routes taken by lionesses in occupying the corresponding final stalking role positions (**a**)

Each individual lioness participating in a hunt was classed in one of seven possible stalking roles (A to G) depending on their final position relative to the observer and prey position (Fig. 1a). Stalking was measured from the start of the hunt until the first lioness charged the prey, or the prey fled. The most common stalking routes taken by lionesses which resulted in the occupation of the corresponding positions are displayed in Fig. 1b. These stalking roles are relative to the position of the prey and the point from which lionesses initially approached the prey, which is also the observer's position. A lioness, irrespective of the hunting group size, could occupy any one of the seven stalking roles in a given hunt and more than one lioness could occupy one stalking role. Without intending anthropomorphism, I have used three terms derived from common games like soccer and rugby (Anon. 1989) to describe the positions of lionesses relative to one another and to the prey. The term "left wing" corresponds to positions A and B, "right wing" to F and G, and "centre" to positions C, D and E in Fig. 1. "Stalk categories", hereafter, refer to "wings" and "centres".

Distances stalked by lionesses were difficult to measure accurately. Rough estimates of stalking distances were made, based on measurements on the vehicle's odometer, during a subset ($n = 278$) of the data. These estimates may not be accurate, but exact distances stalked by lionesses in the different roles were not important to the present analysis. The focus is rather on the pattern of stalking in relation to the prey and other lions. When a lion could not individually be identified, the stalking role it occupied was recorded

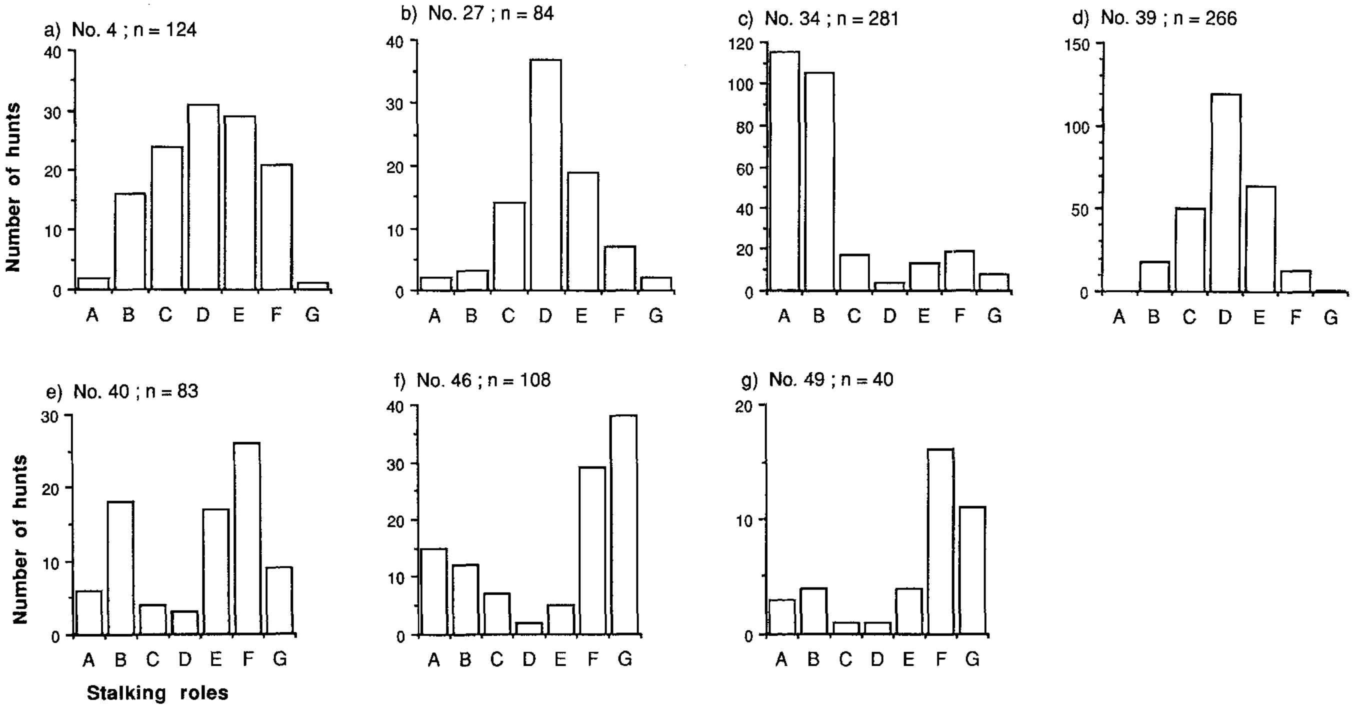

Fig. 2a–g. Stalking roles occupied by seven lionesses of the Okondeka pride, irrespective of the hunting group size or individuals present in the group; $n = 398$. Lionesses showed heterogeneity in occupying stalking roles different from random (G test; $df = 42$; $P < 0.001$)

anonymously. As with most behavioural studies, data could not be normalized and non-parametric statistics (Siegel 1956) were used. All P values are two-tailed.

Results

By means of direct observation, I recorded 486 cooperative hunts (123 hunts were recorded on video tape) in which the stalking roles occupied by individual lions in four prides were noted. The majority of these hunts were on the plains, and the average prey group size was 17 animals (SE = 4.06; $n = 320$; range 1–200). All lionesses present in a hunting group participated in every hunt. From rough estimates, lionesses that occupied "wing" stalking roles stalked an average distance of 320 m (SD = 256; $n = 271$) whereas "centres" stalked on average 30 m (SD = 31; $n = 278$). Nevertheless, all were considered participants as supporting data will demonstrate (see below).

Table 1. Differences between the stalking roles occupied by seven lionesses of the Okondeka pride

Identification number of lionesses	4	27	34	39	40	46	49
4	–	0.11 NS	0.64 ***	0.12 NS	0.24 **	0.44 ***	0.49 ***
27	–	–	0.72 ***	0.05 NS	0.31 **	0.51 ***	0.57 ***
34	–	–	–	0.72 ***	0.52 ***	0.53 ***	0.68 ***
39	–	–	–	–	0.37 ***	0.57 ***	0.62 ***
40	–	–	–	–	–	0.24 *	0.25 NS
46	–	–	–	–	–	–	0.11 NS
49	–	–	–	–	–	–	–

Comparisons between individuals are based on Kolmogorov-Smirnov two-sample tests. P values are two-tailed (NS = not significant; * <0.05; ** <0.01; *** <0.001)

Okondeka pride (Fig. 2)

The stalking roles played by seven adult lionesses of the Okondeka pride were observed during 398 hunts. These hunts represented all observations, including different sub-groups each of which may have consisted of a variety of individuals, and occasionally the entire pride. The seven lionesses showed distinct individual preferences for particular positions in the hunting configuration (Fig. 2), and behaved differently from each other. Lioness No. 34 was a "left wing", Nos. 4, 27 and 39 were "centres" while Nos. 40, 46 and 49 were viewed as "right wings".

To test whether lionesses in these three stalking categories behaved differently from each other, the stalking roles of each lioness were compared (Table 1). "Left wing" No. 34 occupied mostly stalking roles A and B, showing a significant partiality for these stalking roles when compared to all other lionesses. "Centres" (Nos. 4, 27 and 39) occupied similar stalking roles, reflected

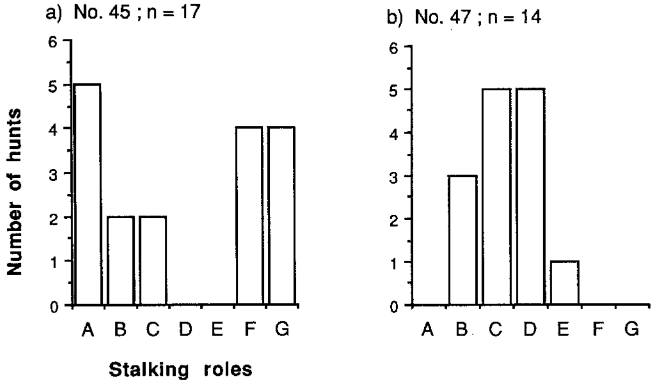

Fig. 3a, b. Stalking roles occupied by two lionesses of the Okaukuejo pride; $n = 20$

by the low $D_{\max}$ values, and they varied significantly from the "left wing" and "right wings". Among the "right wings" (Nos. 40, 46, 49), stalking roles were the same except for a statistical difference between Nos. 40 and 46. Variations in stalking roles filled by individual lionesses at different group sizes are discussed below.

Okaukuejo pride (Fig. 3)

This pride consisted of five lionesses, but due to the difficulty of identifying some individuals, the stalking roles of only two lionesses were recorded (Fig. 3). Lioness No. 45, a "wing", occupied stalking roles on both the left and right sides, while No. 47 frequented the centre roles ($D = 0.47$; $P < 0.05$).

Rietfontein pride (Fig. 4)

Two adult lionesses (Nos. 611 and 612) and four large female cubs, which formed the nucleus of this pride, were all observed hunting in different roles (Fig. 4). None of the large cubs were individually recognizable and the stalking roles they occupied were combined and compared with those of the two adult lionesses. No. 611 formed the "right wing", No. 612 the "left wing" while the large cubs played centre roles (Fig. 4). Both adult lionesses and the cubs behaved differently from each other (Kolmogorov-Smirnov test; $P < 0.05$).

Ombika pride (Fig. 5)

Observations on individual positioning of the six lionesses in this pride were limited (Fig. 5), nonetheless, these observations do show distinction between lionesses. The "left wing" position was filled by No. 37, with Nos. 7, 17 and 36 frequenting "centre" positions. No. 33 tended to favour the "right wing", while No. 13 filled roles both to the immediate left and right of "centre".

Variations within the Okondeka pride

Stalking positions taken up by lionesses of the Okondeka pride are presented in terms of different group sizes and/or individuals present in the hunting group. During 145 of the observed hunts, only two lionesses (Nos. 34 and 39) were present. They were each identifiable by brand marks, and moreover, one of them had a black radio collar. When hunting in this group composition, as in all group configurations for this pride (Fig. 2c, d), lioness No. 34 occupied "left wing" and No. 39 "centre" roles (Fig. 6) ($D = 0.648$; $P < 0.001$).

When comparing the distribution of roles occupied by the two lionesses (Table 2) it appears that these individuals were compensating for variations in each others' stalking roles. When No. 34 played roles on the left side, No. 39 would occupy roles in the centre and to the right of centre, while on the few occasions that No. 34 stalked on the right side, No. 39 would compensate by occupying stalking roles to the left of centre. From an observer's point of view, it appeared that the two lionesses attempted to keep the prey on the imaginary straight line between themselves. The advantage of this behaviour is discussed below.

Lioness No. 40, a "wing", occupied both left and right hand stalking roles (Fig. 2e). During 89 observations the stalking roles of No. 40 were compared to hunts when the "left wing" No. 34 was present, or not present, in the hunting group (Fig. 7). When No. 34 was present occupying the "left wing", No. 40 hunted on

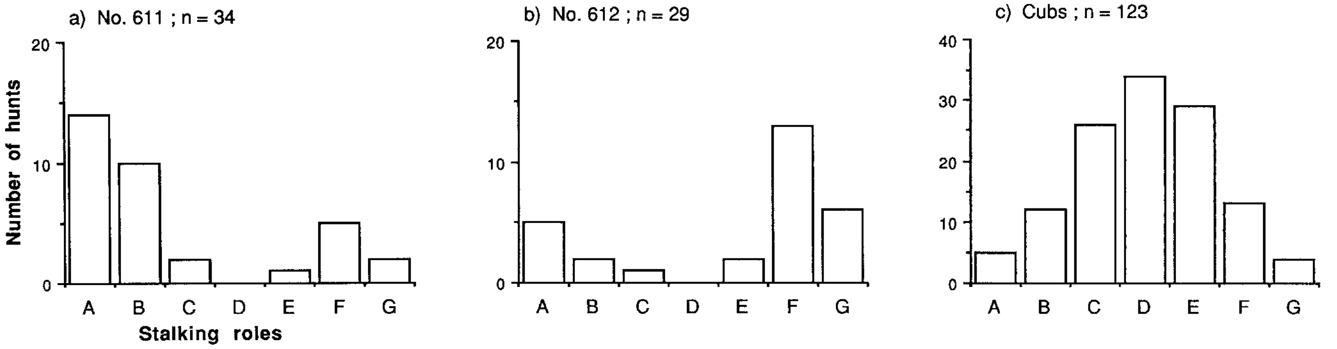

Fig. 4a–c. Stalking roles occupied by two adult lionesses and four large cubs of the Rietfontein pride; $n = 39$. Both lionesses and the cubs occupied stalking roles distinctly different from each other ($G = 99.9$; $df = 12$; $P < 0.001$)

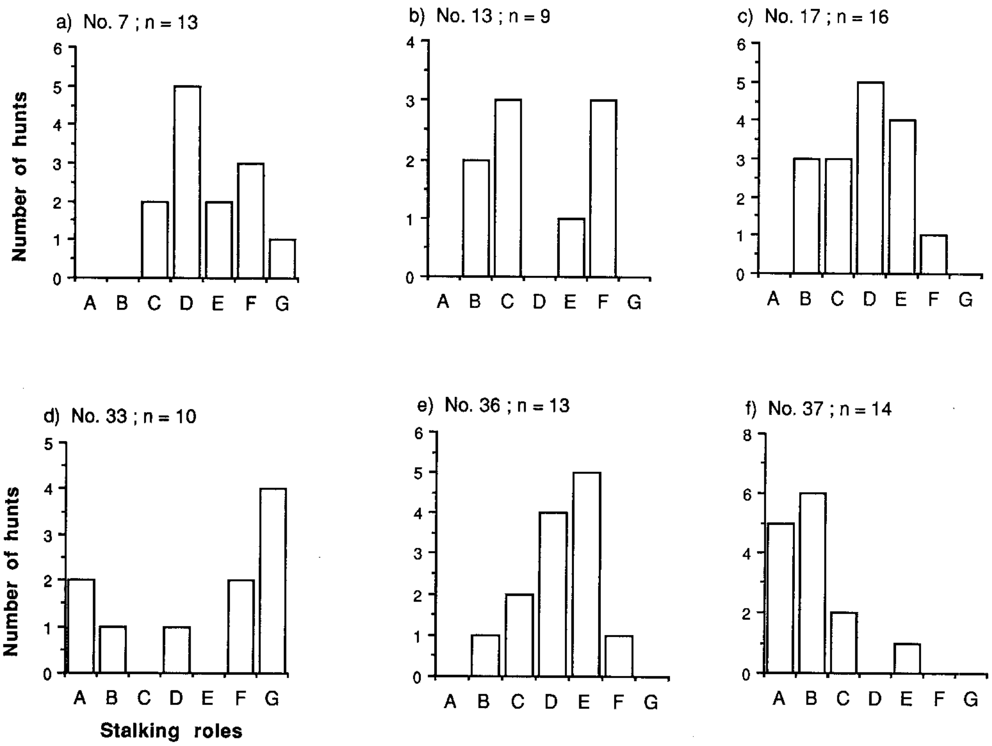

Fig. 5a–f. Stalking roles occupied by the six pride lionesses of the Ombika pride; $n=23$

Fig. 6. Stalking roles occupied by two lionesses of the Okondeka pride, Nos. 34 (*open bars*) and 39 (*shaded bars*), during 145 observations of this group composition

Table 2. Stalking roles occupied by lionesses Nos. 34 and 39 during 145 observations of them hunting together

	Stalking roles	No. 34 A	B	C	D	E	F	G
No. 39	A	0	0	0	0	0	0	0
	B	0	0	0	0	5	4	0
	C	0	0	0	0	5	9	1
	D	34	17	0	0	0	3	2
	E	11	35	8	0	0	0	0
	F	2	4	4	0	0	0	0
	G	0	0	1	0	0	0	0

Pearson $\chi^2=205.1$; $P<0.001$
99% Confidence interval – $P=0.0011$
P values based on exact permutational distributions

the "right wing" side, but when No. 34 was not present No. 40 hunted more often on the left hand side ($D=0.588$; $P<0.01$). This suggests that No. 34 was dominant in occupying stalking roles A and B while No. 40 altered her stalking behaviour accordingly.

Not all females based their stalking patterns on the behaviour of other females. This was particularly true for a young female, No. 73, daughter of the "centre" lioness No. 4 (Fig. 2a), who was observed hunting with the Okondeka pride from the age of 18 months (Fig. 8). Observations on this lioness lasted until the study was terminated when she was 30 months old. No. 73 preferred wing roles, especially "right wing", although she seldom occupied the outer roles, A and G. The roles occupied by No. 73 had a non-significant tendency to differ from the "center" roles frequented by her mother, No. 4 ($D=0.19$; $P>0.1$). The variations in No. 73's stalking roles were independent of the roles occupied by her mother (Pearsons $\chi^2=40.61$; $df=30$; $P>0.05$). During 70 observed hunts, No. 73 was part of a group which included her mother, and Nos. 27 and 46. As with No. 4 the stalking roles played by No. 73 were not related with the positions of either No. 27 or No. 46 ($P>0.1$).

Characteristics and success

When comparing lionesses that frequently occupied "centre" and "wing" stalk-categories in terms of physi-

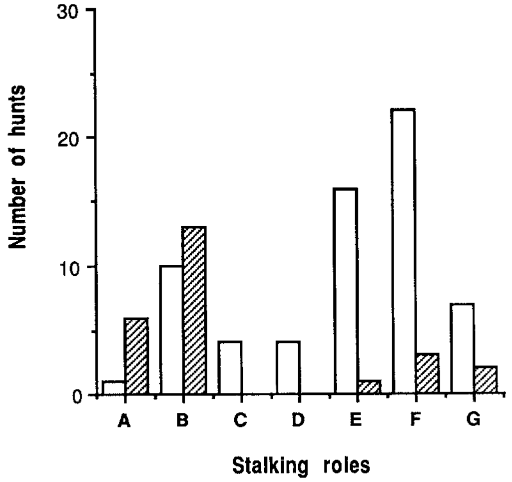

Fig. 7. Stalking roles occupied by the Okondeka pride lioness, No. 40, during hunts when "left wing" No. 34 was present in the hunting group (*open bars*), and when No. 34 was not present (*shaded bars*), regardless of group composition; $n = 89$

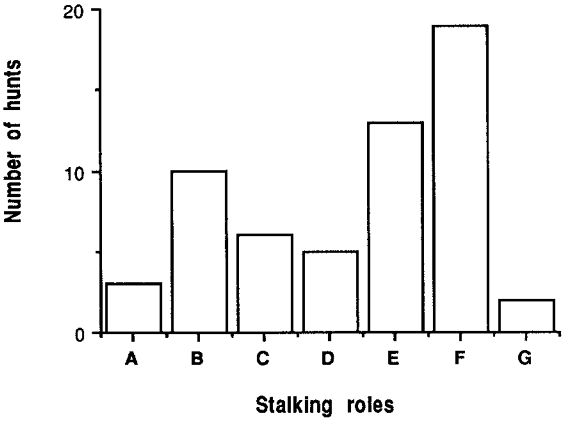

Fig. 8. Stalking roles occupied by the young lioness, No. 73 of the Okondeka pride, between the age of 18 and 30 months, during 58 observations

Table 3. The age, mass, and body measurements of individual lionesses that frequently occupied either "wing" or "centre" stalk catagories

Stalking roles Nos.	% of hunts individual played indicated role	Age[a] (Years)	Mass (kg)	Body measurements		
				Shoulder height (cm)	Heart girth (cm)	Body length (cm)
"Wings"						
34	88	6–9	145	93	105	167
37	79	6	139	91	101	169
40	71	5–8	130	85	96	152
45	88	6	118	84	103	157
46	87	7–10	132	91	95	157
49	85	5–8	134	85	96	152
611	91	6	130	95	103	173
612	89	5	117	83	90	150
Mean			130.6	88.4	98.6	159.6
SD			8.9	4.3	4.8	8.2
"Centres"						
4	68	8–11	138	94	106	166
27	83	9–12	152	92	111	168
39	83	7–11	147	92	110	164
47	79	5–6	136	90	104	161
Mean			143.3	92	107.8	164.8
SD			6.4	1.4	2.9	2.6
Mann-Whitney $U=$		5.5	4.0	9.0	1.0	11.0
		n.s.	$P<0.05$	n.s.	$P<0.01$	n.s.

[a] The age estimates for some individuals are broad because they were observed continuously over a period of up to 4 years

cal characteristics (Table 3), there were no statistical differences between the age, shoulder height and body length measurements of the two groups. Lionesses reach the asymptotes of their growth curves at roughly the age of 5 years (Smuts et al. 1980). "Centre" lionesses did, however, appear somewhat older ($P = 0.069$), heavier ($P < 0.05$) and larger than "wings". The former have larger heart-girth measurements ($P < 0.01$) than "wings".

On the plains of Etosha N.P., lions had a low average capture success of 15% for all species and hunts observed in both the dry and wet seasons (Stander 1992). With single lionesses mostly unsuccessful in capturing large and fleet-footed prey (2.3%) they are expected to

Table 4. The frequency that "centre" and "wing" lionesses of the Okondeka pride attacked prey[a]; by initiating a chase or participating in a chase, and captured prey[b] either by "ambush" or "rush"

	Attack prey		Capture prey	
	Initiate chase	Participate in chase	"Ambush"	"Rush"
"Centre" lionesses (Nos. 4, 27, 39)	28	48	29	5
"Wing" lionesses (No. 34, 40, 46, 49)	66	41	12	24
Fishers exact probability test	$P=0.0003$ $n=183$		$P<0.0001$ $n=70$	

[a] Initiate chase = The first lioness to charge at prey
Participate in chase = Subsequent lioness joins the chase after it has been initiated

[b] "Ambush" = The position from which a lioness captures prey fleeing from another lioness
"Rush" = Lioness initiates an attack and captures prey after a chase of up to 150 m

be cooperative hunters (Packer and Ruttan 1988). Cooperative hunts had a high success rate of 27%, increasing with hunting group size ($r_s=0.821$; Stander 1992; Stander and Albon in press). This cooperation is further reflected by the methods of prey capture. During successful cooperative hunts on the large and fleet-footed prey, lions captured 73% ($n=92$) of the prey from an "ambush" position. The lioness in "ambush" captured the prey by leaping at it or rushing a short distance, frequently <10 m ($n=57$), but seldom >10 m (Binomial test: $n=81$; $x=24$; $P<0.001$). The remaining 27% of the large and fleet-footed prey were pursued and captured by lionesses during a "rush" of 20–150 m.

The rate of injury to lionesses during prey capture was low. No sign of injury to the hunter was detected during the 63 observed kills on adult springbok. Of the 25 large prey kills observed, the lioness capturing the prey was injured on two (8%) occasions. The wounds were minor and superficial and did not appear to affect the lioness' behaviour thereafter. On seven occasions when an adult zebra was able to free itself from the grip of a lioness, by kicking or falling onto her, no noticeable injuries to the lioness were observed.

During observations of attacks on prey animals by the Okondeka pride, the behaviour of individual lionesses was recorded (Table 4). "Wing" lionesses initiated attacks on prey significantly more often than "centre" lionesses ($n=183$). "Centre" lionesses participated in subsequent attacks on prey more often than "wings", by chasing prey after another lioness had initiated the attack. During 70 observations of prey capture, "centre" lionesses were observed to capture prey from an ambush position significantly more often than "wings" (Table 4). Lionesses that occupied "wing" positions captured prey most often during a rush. When all successful hunts by the Okondeka pride are combined; "centre" lionesses captured prey slightly more often than "wings" ("centres" = 34; "wings" = 26) ($\chi^2=0.313$; n.s.).

To assess whether hunts were more successful when lionesses played their preferred roles, their attendance in these stalking roles was rated on a relative proportion scale (Fig. 9). Hunts where the preference rating was >0.5 (more than half the lionesses present were in their preferred stalk category) had a success rate of 17% ($n=337$), whereas hunts with a preference rating ≤ 0.5 had a lower success rate of 7% ($n=61$). The binary dependent variable (hunting success) was related to the preference rating, and the probability of hunting success calculated using a generalized linear model (Albon et al. 1986). The logistic model suggests that hunts where most

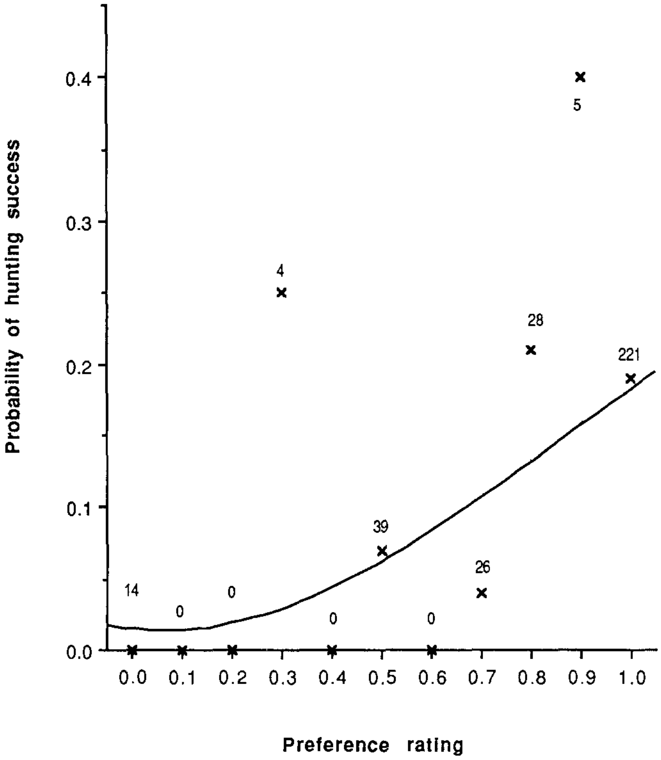

Fig. 9. A logistic curve representing the probability of hunting success at different preference ratings. Each hunt was assigned a preference rating (p/N); where p = the number of lionesses in their preferred hunt-catagories; and N = the total number of lionesses participating in the hunt. Thus, if all the lionesses present were in their preferred stalk categories the preference rating would be 1. Since raw data are binary (either 0 or 1) the success rates for hunts in each 0.1 interval of the preference rating are shown, with *sample sizes*

lionesses present occupied their preferred stalk category ("wing" or "centre") had a higher probability of success ($\chi^2 = 8.5$; $df = 1$; $P < 0.01$) (Fig. 9). By including lioness group size in the model, a significant increase in the deviance was found ($\chi^2 = 10.7$; $df = 1$; $P < 0.01$) and provided a significantly better fit ($\chi^2 = 19.2$; $df = 2$; $P < 0.001$). This suggests that group size is an important variable while preference rating remains a significant factor influencing hunting success. Most likely to succeed are hunts in large groups where most individuals are occupying their preferred stalking categories.

During 156 observed prey captures, the lioness that captured the prey always killed it. Killing was the procedure whereby a lioness suffocated the prey (Schaller 1972). Other lionesses present often started feeding before the prey was dead. During only four kills (2.6%) did a second lioness assist in the killing procedure.

Discussion

Lionesses in all four prides repeatedly occupied particular stalking roles during cooperative hunts. The unequal participation by individuals suggests individual variability, exemplified by lionesses in the same pride occupying different stalking roles. Lionesses in this study, showed distinct behavioural differences in two major categories: "wings" and "centres". Lionesses that occupied the "centre" stalking roles usually stalked very short distances and mostly lay watching the prey and the stalking activities of the "wings". These data show that lionesses hunt cooperatively by division of labor with the "left and right wings" circling the prey and "centres" lying in a position from which they may catch prey fleeing from the "wings". Within the context of this hunting behaviour, I do not presuppose conscious decision-making by individuals.

Cooperative hunting with "drivers" and "catchers" has been described by Guggisberg (1962), Schaller (1972) and Griffin (1984) but has not previously been supported with sufficient data. The individually distinct hunting strategies by lionesses observed on the open plains of Etosha N.P. could not be due to constraints of the terrain because of the homogeneity and general lack of cover. Scheel and Packer (1991) found no relation between stalking patterns and available cover during communal hunts by lions in the Serengeti.

Scheel and Packer (1991) show that a substantial proportion of lionesses "refrain" from participation in communal hunts by stalking very short distances and not participating in the final stages of the hunt. This behaviour was common in males and observed in females during hunts on species where the success rate for single lionesses was high (Scheel and Packer 1991). The Etosha lionesses are expected to be more cooperative than those in the Serengeti, and less likely to "cheat" (Packer and Ruttan 1988). Repeated observations of the behaviour of individually known lionesses at Etosha support these hypotheses, and show that even though "centres" stalk very short distances in relation to "wings", they are most often responsible for capturing prey from an "ambush" position which is the primary means of capturing large and fleet-footed prey. Lionesses that occupy "wing" positions, on the other hand, stalk further and often initiate an attack on prey.

According to body measurements it would appear that "centres" are of a stockier build. This apparent physical difference, although speculative, could be explained by behavioural idiosyncrasies between the two categories of hunters. Although no accurate measures of the distances stalked by individual lionesses were possible, it is, however, quite clear that "wings" stalk substantially further than "centres". The stockier "centres" participate in most chases initiated by "wings" and capture prey more frequently from the ambush position. Their apparently heavier build may furthermore be advantageous in negotiating the capture of oncoming large and fleet-footed prey.

The stalking roles occupied by individual lionesses appear sensitive to a number of variables. Sample sizes of hunts by the Okondeka pride were sufficient to look at only a few variations. Firstly, during 145 hunts where the same two lionesses (Nos. 34 and 39) were foraging together, the stalking role occupied by one was dependent on the role occupied by the other. It would appear that the two lionesses coordinated their positions so as to keep the prey between them; therefore, keeping the third point (the prey) on an imaginary straight line connected between the two lionesses. The importance of this behaviour is illustrated by the following description: If one lioness charges, the prey could flee in the direction of the second lioness, who will then be in an "ambush" position to capture the prey. Secondly, the stalking roles occupied by lioness No. 40, in hunts of all group sizes, varied substantially between hunts in which No. 34 was present or not present in the hunting group. From the limited sample available it appears that lionesses adjust their tactics in each hunt, in response to the presence, absence and position of other individuals.

A young Okondeka pride lioness was observed from the age of 18 months when she was first seen hunting, and the process by which her hunting skills were acquired exemplifies the complexity of the development of cooperative hunting strategies. Rather than imitating the older lionesses, No. 73 occupied stalking roles very different from those of her mother (No. 4) and two other lionesses (Nos. 27 and 46) who were present during most of the observed hunts. The stalking activities of this lioness, and four large cubs in another pride, appeared to be an acquired behaviour (Alcock 1989), through watching the hunting activities of all the adult lionesses of the pride (Eaton 1970).

Cooperative hunting in a semi-arid environment

In parts of East Africa, where ungulate and carnivore biomass is high (East 1984), the hunting success of solitary lions ranges between 11 and 29% (Schaller 1972; Elliot et al. 1977; Van Orsdol 1981). On the open and flat terrain of Etosha N.P. where small pockets of prey occur at a low density (East 1984) the hunting success of solitaries was much lower, suggesting that Etosha lions should more often hunt in groups (Packer and Ruttan 1988). Cooperative hunting by division of labor may have developed within the context of the semi-arid conditions of Etosha N.P.

The apparent advantages of group hunting at Etosha are discussed briefly. During the wet season lionesses in all group sizes, including solitary females, acquired daily food intake above the estimated minimum requirements of 5–8.5 kg (Packer et al. 1990). The 8-month-long dry season, however, proved to be a period of food deprivation and lionesses acquired significantly less food per day than in the wet season (Stander 1992). Solitaries did not meet the estimated daily food requirements and infrequently foraged alone. Lionesses hunted in groups, where the hunting success increased with larger numbers of lionesses. Cooperative hunts were more successful than non-coordinated group hunts (Stander 1992) and hunting success was further improved when lionesses hunted in their preferred stalk categories. The advantages of cooperative stalking are illustrated by the fact that most prey were captured from an "ambush" position, which required coordinated stalking and pursuit of large and fleet-footed prey in an open habitat.

While it has been suggested that lions hunt in groups to subdue and kill large prey (Schaller 1972; Bertram 1979; Lamprecht 1981), evidence from the present study reveals that the lioness that captured prey up to the size of an adult zebra also subdued and killed the prey (also see Stander 1992). The rate of injury to lions during prey capture was low. Nonetheless, cooperation under the described conditions, was essential in order to capture large and fleet-footed prey, which formed >80% of their diet. Larger prey such as buffalo (*Syncerus caffer*) and giraffe, however, may require a cooperative effort for lions to subdue and kill them (Packer 1986).

Group hunting and cooperation, in the Etosha N.P. context, suggest clear benefits to the individuals' feeding efficiency and that cooperative hunts where lionesses occupied their preferred positions were more successful. The complex hunting strategies involving division of labor in lionesses, described in this paper, may have evolved from the fundamental advantage of higher per capita food intake derived from cooperative hunting during the dry season (Stander 1992).

A controversy exists as to the extent to which non-human animals are capable of conscious decision-making (Griffin 1984). In a single example of cooperative hunting, Griffin (1984) speculates that lionesses coordinated their stalking patterns by taking conscious advantage of the locations of others. Whether or not the present study reveals a level of mental awareness not previously documented in non-human animals, it does indicate that measurable benefits come from cooperative hunting in this population.

Acknowledgements. The Ministry of Wildlife, Conservation and Tourism provided logistical and financial support during the study. I am grateful to Drs. E. Joubert, H.H. Berry, M. Lindeque, W.C. Gasaway, Mr. T.B. Nott and Mr. J.L. Scheepers for their support during various stages of the field work. The National Geographic Society kindly provided an infra-red video camera and Mrs Holly Stander is thanked for her contribution in recording hunting behaviour on video tape. The Cornell Laboratory of Ornithology provided logistical support during data analysis, and I am especially grateful to Mrs Katy Payne and Dr. C. Walcott. Mr. D. Andrews provided advice on statistical problems. Drs. Craig Packer and D.R. Griffin, Dave Scheel, Karen Laurenson and two anonymous referees provided valuable criticisms on earlier drafts.

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