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Hunting success of lions in a semi-arid environment

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Synopsis

Parameters that influence the hunting success of lions in a semi-arid region in Namibia were assessed by means of generalized linear models. Results indicate that when combined, hunting techniques employed by lionesses, lioness group size, prey species, time of day (day/night), terrain, and the interaction between terrain and day/night had significant independent effects on the probabiliry that a hunt would be successful. Hunts that involved co-ordinated stalking were more likely to succeed than other hunt categories. Success of hunting the five major prey species increased linearly with lioness group size. Lionesses were also more successful during hunts on moonless nights in undulating terrain. Under the semi-arid conditions in Namibia, where lions are exposed to eight months of food scarciry in an open habitat, group hunting and co-ordinated co-operation are the most important variables influencing the outcome of hunts and therefore also *per capita* food intake. In this environment group hunting may be an important factor in the evolution of socialiry in the species.

Introduction

The foraging behaviour of the lion *(Panthera leo),* the only social felid, has recently attracted considerable attention. Grouping patterns, foraging

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success and co-operative hunting have been discussed in terms of optimal foraging theory and possible causes for the evolution of sociality. Group hunting has been interpreted as an attempt to m~ximize *per capita* food intake, minimize starvation and therefore improve foraging success (Schaller 1972; Caraco & Wolf 1975; Clark 1987), especially in open terrain and when prey are widely dispersed (Wilson 1975; Macdonald 1983). Most authors used data from East Africa, and usually those collected by Schaller (1972) in the Serengeti. However, Packer (1986) pointed out that Schaller's data are not suitable for the analysis of foraging success in relation to group size and presented new data from the Serengeti showing that lions did not forage in groups of sizes that would maximize *per capita* food intake (Packer, Scheel & Pusey 1990).

Elsewhere in Africa the behaviour of lions may be highly variable because of different ecological constraints (Sunquist & Sunquist 1989). For example, hunting success rates have been recorded at 15% in Etosha National Park (N.P.) (Stander 1992a), 23% in Serengeti N.P. (Schaller 1972), 29% in Queen Elizabeth N.P. (Van Orsdol 1981) and 38% in Kalahari Gemsbok N.P. (Eloff 1984). Van Orsdol (1984) presented elaborate data on various prey-, lion- and environment-related factors which affect the hunting success of lions, and suggested that factors such as vegetation cover, prey group size and prey body size may influence their foraging behaviour.

Logistic regression models (McCullagh & NeIder 1983; Albon *et al.* 1986) were used to assess data on the hunting behaviour of lions living at a low density (1.82-2.0 animals per 100 km2) in a semi-arid environment in Etosha National Park, Namibia (Stander 1992a, b), in order to determine the important variables that influence hunting success. An analysis of these factors attempts to contribute to an understanding of the dynamics of lion foraging behaviour and aspects of the evolution of social behaviour in the speCIes.

Study   area

Etosha National Park (190 S 160 E) is located in northern Namibia, bordering three major biotic zones: the Southern Savanna Woodland, the South-West Arid and the Namib Desert (Skinner & Smithers 1990). Etosha occupies an area of 22 270 km2 with a mean annual rainfall of 351 mm. Open surface evaporation rate averages 2700 mm year-I. Temperatures range from -1 °C Uuly) to 41 °C Uanuary), as measured at Okaukuejo in the centre of Etosha (Etosha Ecological Institute unpubl. data). There is a wet season Uanuary-May) and a dry season Uune-December). During the wet season an estimated 4300 zebra *(Equus burchelli),* 10000 springbok *(Antidorcas   marsupialis),* 2500 wildebeest *(Connochaetes   taurinus)* and

1500 gemsbok *(Oryx gazella)* (Gasaway, Mossestad & Stander 1991) concentrate on the short-grass plains (Le Roux *et al.* 1988), and disperse into the woodland areas towards the end of the dry season. Five lion prides inhabiting the short-grass plains which surround the saline Etosha Pan were observed betweeh May 1984 and August 1988.

Methods

Lions were directly observed from a vehicle at distances of 20-100   m. At night lions were viewed with equipment suitable for low light conditions. A detailed description   of methods used is presented elsewhere (Stander 1992a). Lions were immobilized (Van Wyk & Berry 1986; Stander & Morkel1991)   and permanently marked (Orford, Perrin & Berry 1988) and radio-collars were attached to between one and three lionesses from each pride. Radio-collared   animals were located by ground and aerial tracking. Lions were followed and observed for 52 periods ranging between one day (24 h) and 15 days. All observations   were recorded on a tape-recorder   or filmed using an infra-red-sensitive   video camera.

Defining a hunt is difficult, and may affect calculations of hunting success (Kruuk 1972; Schaller 1972; Mills 1990). In the present study lions were considered to have hunted when, after staring at the prey with alert facial expressions and posture (Schaller 1972), they stalked more than 10 m, only abandoning   the hunt when the prey fled.

During each hunt *(n =* 840), data were collected on the following factors which may have influenced the outcome.

Prey-related factors

Prey species

Lions hunted 16 species of prey, but only five species made up 95% of the hunts. Analyses were confined to hunts of these five species, namely springbok *(n =* 621 hunts), zebra *(n =* 135), wildebeest *(n =* 56), gemsbok *(n =* 16) and springhare *(n =* 12).

Lion-related factors

Prides

Hunts by five different prides *(n =* 604, 123, 50, 44, 12) inhabiting the plains, were observed. Pride sizes ranged between 1-4 males, 4-7 females and 0-9 cubs.

Lion group size

The number of lionesses two years of age and older was recorded   during each hunt. Two-year-old   lionesses are known to be competent   hunters

(Schaller 1972; Packer *et al.* 1990). Group size during hunts varied from one to seven.

Hunt class

Hunts were classed into three basic categories: class A-single   lionesses or groups stalk directly at prey $(n = 187)$; class B-group   hunts where some individuals spread out in an attempt to surround the prey, but do not co-ordinate   their stalking   behaviour $(n = 228)$; class C-group   hunts of co-ordinated   co-operation   in which some lions encircle the prey and often charge, causing the prey to run towards other lions $(n = 313)$. Detailed descriptions   of these hunt classes have been given elsewhere (Stander 1992a).

Environment-related factors

Season

All hunts were grouped as either wet-season $(n = 345)$ or dry-season $(n = 495)$.

Day/night

Data were classed on an illumination   scale, where $1 =$ daylight $(n = 32)$, $2 =$ moonlit nights $(n = 219)$, $3 =$ moonless nights $(n = 589)$. During nocturnal hunts the phase of the moon, and whether it was up or down, was recorded   in the field and correlated   with the Astronomical   Almanac (Planetarium,   South Africa).

Terrain

Hunts were divided into five categories of terrain according to vegetation type (Le Roux *et al.* 1988) and average height structure: (a) short grass plains with grass height:S;; 10 cm $(n = 626)$; (b) Okondeka   duneveld, which consists of broken undulating sandy terrain with short grass < 20 cm in height $(n = 18)$; (c) saline pan, supporting no vegetation $(n = 34)$; (d) dwarf shrub savanna, containing sparsely spaced shrubs < 60 cm in height, on flat terrain   covered with short grasses $(n = 117)$; and (e) acacia thickets, dense stands   of between   1 and 2 m in height $(n = 42)$.

Wind speed

Data on wind speed $(n = 603$ hunts) were obtained from a weather station, where wind speed was measured on the plains 2 km north of Okaukuejo. Lions were usually observed less than 20 km from the weather station, but occasionally up to 30 km. Because of the flatness of the area (Le Roux *et al.* 1988) it was assumed that wind speed was consistent within 30 km of the station. Data on wind direction were limited and therefore not incorporated

in the present analyses. The influence of wind direction on the outcome of hunts has been discussed elsewhere (Stander 1992a).

Data analysis

The relationship between hunting success, a binary dependent variable (success $= 1$, or unsuccessful $= 0$), and the above-mentioned independent variables was described by standardized logistic curves (see Albon *et al.* 1986). To test whether each of the variables (pride, hunt class, lioness group size, prey species, day/night and terrain) had a significant effect on the probability of a hunt being successful, logistic regression models of the form:

$$P(Y_i = 1) = \frac{\exp (A + B_1x_i1 + B_2x_{i2} + B_3x_{i3} + B_4x_{i4} + B_5x_{i5} + B_5x_{i6} + B_5x_{i7})}{1 + \exp (A + B_1x_i1 + B_2x_{i2} + B_3x_{i3} + B_4x_{i4} + B_5x_{i5} + B_5x_{i6} + B_5x_{i7})}$$

where

A, Bh *B2, B3, . . . Bs* $=$ constants
Xil $=$ pride
Xi2 $=$ Hunt class (A, B, C)
Xi3 $=$ No. of lionesses (1-7)
Xi4 $=$ Prey species
XiS $=$ Day/night (day, moonlit night, moonless night)
Xi6 $=$ Terrain
X,7 $=$ Day/night interaction with terrain
      $= 1,2,3 \ldots 840$

were fitted by means of a generalized linear model (McCullagh & Nelder 1983). Parameters of the logistic regression model were estimated by maximum likelihood to determine whether the inclusion of extra parameters in the model significantly improved the fit. This was done by comparing differences between the deviance values of different models (analogous to sums of squares), and then using X2to test for significance at 5%. Degrees of freedom were calculated as the difference in the number of parameters fitted to the two models being compared. By calculating the coefficients in this linear function, probability values of hunting success for each hunt could be determined.

In order to illustrate the independent effects of each variable on the success of hunts, all other variables were set to a constant. These were chosen on the basis of larger sample sizes and, where applicable, the median of observations. The constants were hunt class $=$ C, the median number of lionesses (3), prey species = springbok, day/night = moonless night, terrain = plains, and day/night terrain interaction $=$ moonless night and plains.

The effects of wind speed on hunting success were tested in a new model
(d.f. = 485). Because the sample sizes were very low we excluded hunts on
gemsbok and springhare. This model was equivalent to previous models and
included the terms of the 'best' model on which other analyses are based.

Results

The general model

Six parameters-hunt   class, number of lionesses, prey species, day/night,
terrain and the interaction between terrain and day/night-were   combined
in a model (H, Table 1) that explained more of the deviance than any other
combination of variables. Each term in this, the 'best' model, had significant
independent   effects on the goodness-of-fit of the model (Table 1) and
therefore influenced the probability that a hunt was successful. Hunt class
was the most important variable, followed by the number of lionesses, the
day/night terrain interaction,   and prey species.

Effects of variables on hunting success

Differences in hunting success between prides
There were significant differences between prides when pride effects were
considered   alone (mean probability   values = 0.07, 0.08, 0.09, 0.15 and
0.30 respectively). These differences between prides persisted when hunt
class, number of lionesses and prey species were added to the model.
However, the incorporation   of the day/night parameter   in the model
accounted for most of the variation between prides and these differences
were no longer significant (Model E vs F; $X2 = 8.7$; *d.f. = 4*; N.S.; Table 1).

Number of lionesses and hunting success
When lioness group size was incorporated   into the model as a categorical
variable (1, 2, 3 ... 7) there were significant differences in the hunting
success of different group sizes. Coefficients of the parameters   in this model
increased linearly, indicating that hunting success was greater in larger
groups (Fig. 1). The improvement   of treating group size as a categorical
rather than a continuous   variable was not significant $(X2 = 6.2$; *d.f. = 5*;
N.S.). Therefore   a linear term for the number of lionesses was used
throughout. The probability of a successful hunt increased with lioness
group size for all five prey species (Fig. 2). When constants   were set at hunt
class C, with lionesses hunting springbok on the plains during moonless
nights, solitary lionesses had a 0.124 probability of success. This probability
increased linearly to 0.518 when lionesses hunted in groups of seven.
When the variables season and the interaction   between season and
number of lionesses were added to the model H, the deviance did not

Table 1. Goodness-of-fit tests for logistic models of different variables that influence hunting success. Numbers in each model indicate which variables have been included[a]

				Interaction day/night-terrain						
A	1								4	;
B	1								2	:
C	1		3						1	.
D	1		3						4	;
E	1		3						2	*
F			3						4	***
G			3						4	N. S.
H			3						8	*
I					7	5			4	***
J					7	5			4	N. S.
K					7	5			1	***
L					7	5			2	***

[a] Each model is compared with the model in the previous row, except that models J, K and L are compared with the model H. Significant tests (χ^2) refer to the inclusion or deletion of a single term, indicated by the number in the test variable column. The model H is the best model, and was used for subsequent interpretation.

N. S. = not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$
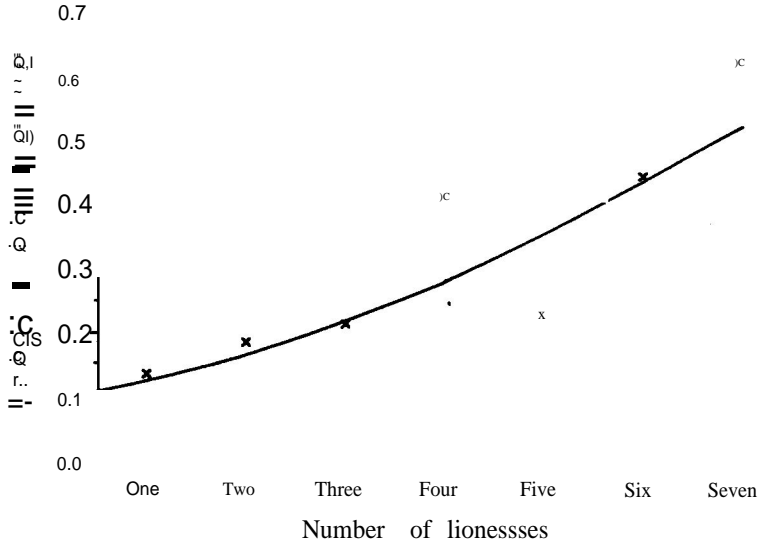
Fig. 1. Probability of hunting success plotted against lioness group size. Crosses indicate values
for group size fitted as a categorical variable while the regression line fitted through all the
individual data points shows the linear trend. Constants were set at class C hunts of springbok
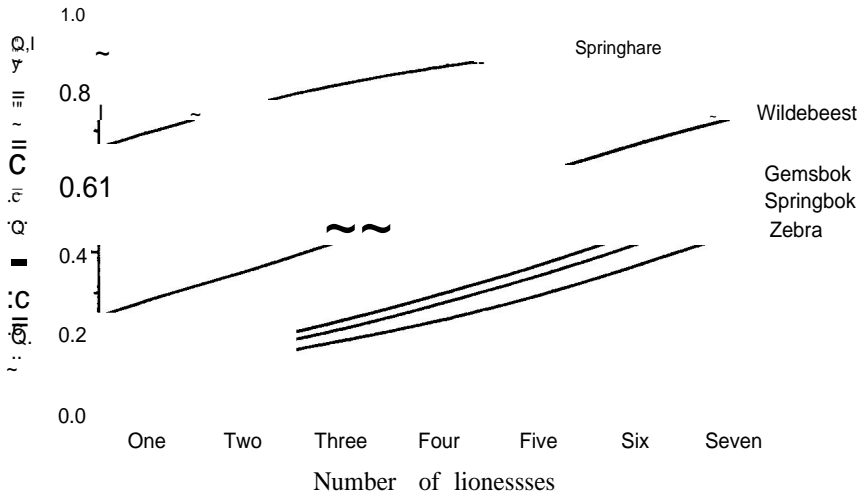during moonless nights on the plains.

Fig.2.   Logistic curves indicating the probability of hunting success on five prey species plotted
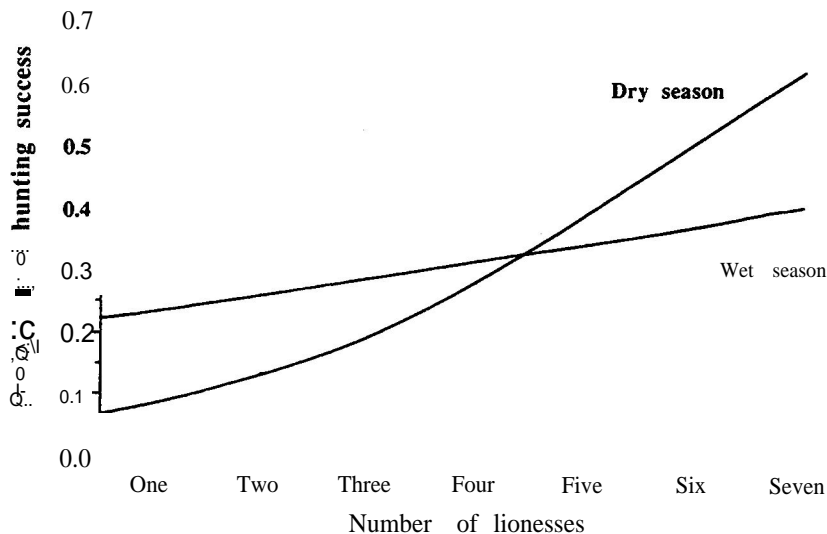against lioness group size. Constants were set at class C hunts during moonless nights on the
plains.

Fig. 3. Logistic curves indicating the probability of hunting success during the wet and dry season plotted against lioness group size. Constants are the same as those given in Fig. 1.

increase significantly ($X2 = 5.1$; *d.f.* $= 2$; $P < 0.1 > 0.05$). However, the probability of success increasing with group size tended to be more pronounced in the dry season than in the wet season (Fig. 3).

Prey species and hunting success
Probability curves of hunting success by different lioness group sizes were similar for springbok, zebra and gemsbok (Fig. 2). Hunting success on wildebeest, however, was higher, with solitary lionesses showing a 0.281 probability of success which rose to 0.747 for groups of seven. Springhare hunts were most successful. The probability of success for single lionesses was 0.84, increasing to 0.899 for groups of five lionesses, the maximum group size that hunted this species.

Hunt class and hunting success
Class C hunts had the highest probability of success (Fig. 4) followed by class A and then B. Groups of three lionesses, when hunting springbok on the plains during moonless nights, show a 0.218 probability of success when employing co-ordinated co-operative hunts (class C). The high probabilitY of success for class A hunts, which are less co-operative than either B or C, is confounded by the fact that lionesses mainly capture springhare and vulnerable neonates using this method (Table 2).
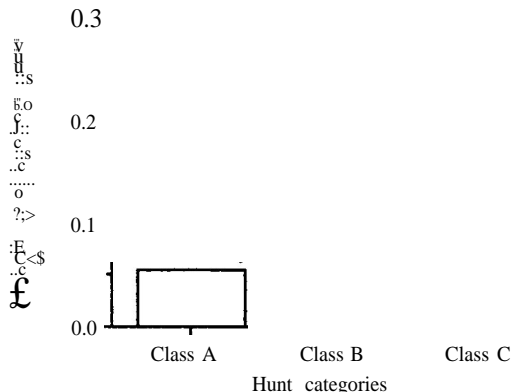
Fig. 4. The probability of success for three hunt classes. Hunt classes represent behavioural categories: Class A = one lioness, or a group of lionesses each behaving similarly, stalk directly at prey; Class B = lionesses partly encircle prey but fail to co-ordinate stalking patterns;   Class C = co-ordinated   co-operation   where some lionesses encircle prey while others wait for prey to move towards them. Constants were set at springbok hunts by groups of three lionesses during moonless nights on the plains.

Table 2. The distribution of kills, grouped either as 'neonates and springhare,a or 'large and fleet-footed prey,b, in relation to several variables that affect hunting success

	Neonates and springhare kills (%)	Large and fleet-footed prey kills (%)	Total kills (n)
Class A[c]	91	9	23
Class B	13	87	8
Class C	12	88	86
Day	64	36	11
Night			
Moonlit	32	68	25
Moonless	20	80	92
Terrain			
Thickets	57	43	7
Scrub	21	79	24
Plains	23	77	78
Pan	80	20	10
Duneveld	38	62	8

[a] Neonates and springhare are potentially vulnerable prey because they are hunted with a high rate of success. Neonates refer to the vulnerable young of springbok, zebra, wildebeest and gemsbok.
   Large and fleet-footed prey are adult and 'capable' juvenile zebra, wildebeest, gemsbok and springbok.
[c] See text and Fig. 4 for definitions of hunt classes.

Time of day, terrain and hunting success

The time of day that a hunt takes place also influences the probability that it will be successful. Terrain is less important, but the interaction between day/ night and terrain has a strong influence on hunting success (Fig. 5). Hunts during moonless nights, when most prey were killed (Table 2), have the highest probability of success in the Okondeka duneveld (0.924) although all terrain types, except thickets, have probability values higher than 0.2. During moonlit nights the probability of success on the plains (0.004) and saline pans (0.0009) is very low because prey could detect stalking lions. However, in the thickets, dwarf scrub savanna and Okondeka duneveld, hunting success rose to above 0.2. Presumably these areas provide sufficient stalking cover for lionesses when hunting the large and fleet-,footed prey that made up the majority of kills on these nights. Conversely, daytime
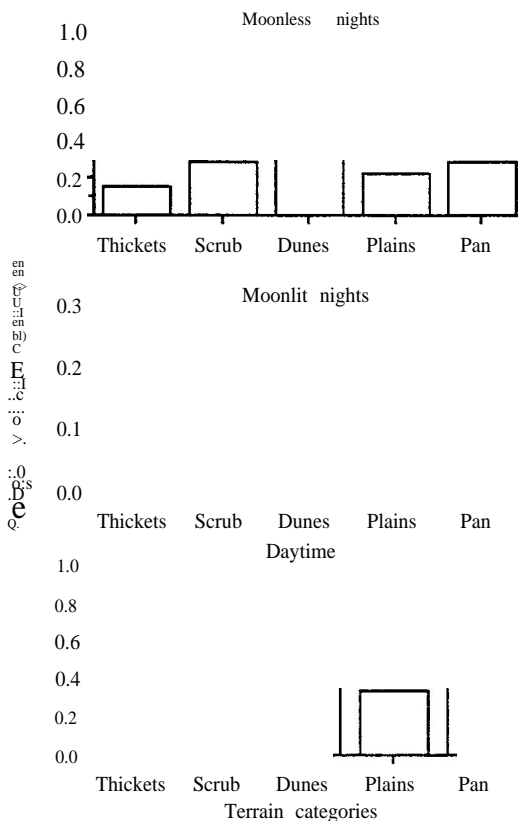

Fig.5. The probability of hunts being successful in five types of terrain during the day, moonlit nights, and moonless nights. Constants were set at class C hunts on springbok by groups of three lionesses.
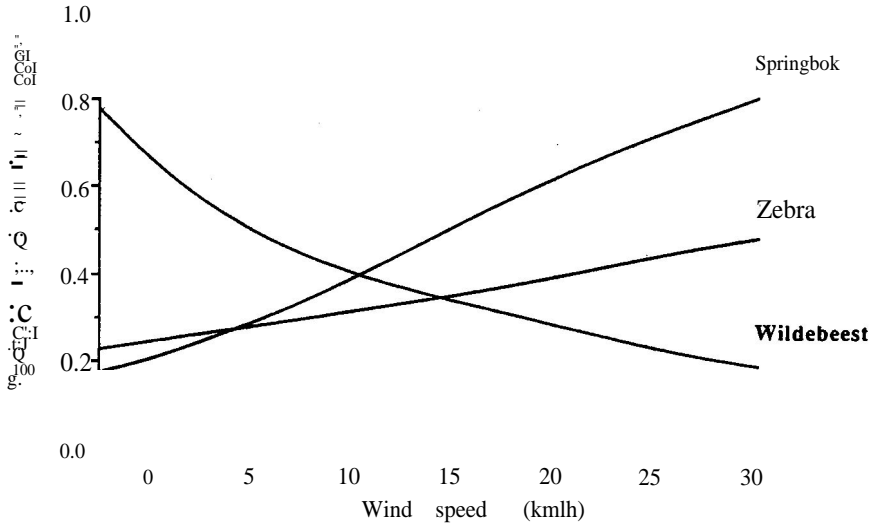
Fig. 6. Logistic curves indicating the probability of success of hunting springbok, zebra and wildebeest, at different wind speeds. Constants were set at class C hunts by groups of three lionesses, during moonless nights on the plains.

hunts are most successful on the saline pans (0.943), duneveld (0.562) and plains (0.326). These results, however, are confounded by prey vulnerability (Table 2). Over 90% of the prey killed during the day were neonates. Lionesses spotted vulnerable prey over long distances (because the terrain was open and flat) and then easily approached and captured them.

Wind speed and hunting success
Hunting success generally increased with rising wind speed. By adding wind speed to a new model, similar to the 'best' model (H, Table 1), the deviance increased significantly $(-l = 6.3; d.f = 1; P < 0.02)$. This model was further improved by adding the interaction of wind speed with prey species $(l = 7.3; d.f = 2; P < 0.05)$. During hunts of springbok and zebra the probability of success increased with wind speed (Fig. 6). However, a negative relationship is evident for hunts of wildebeest.

Discussion

Co-ordinated group hunts and lioness group size are the two most important variables in determining the success of hunts. In all prey species the probability of success increased linearly with lioness group size. Previous studies of lion hunting behaviour have not illustrated such a strong

relationship between hunting group size, co-operation and hunting success as that presented in this paper (Gittleman 1989; Packer *et al.* 1990). Schaller (1972) showed that pairs were twice as successful as single lionesses, but that success did not improve with larger groups. Van Orsdol (1984) found a significant increase in hunting success for groups larger than two in one area, and groups larger than three in another area, whereas Elliot, Cowan & Holling (1977) observed no differences.

We suggest several reasons why lionesses in Etosha N.P. are more successful when hunting co-operatively in large groups than lionesses in other areas.

First, hunting success of solitary females (2.5%; Stander 1992a) is low compared to other studies (11-29%: Schaller 1972; Elliot *et al.* 1977; Van Orsdol 1981). Therefore, according to theoretical models by Packer & Ruttan (1988), Etosha lions ought to co-operate more.

Second, vegetation cover is known to be a crucial variable that influences the outcome of hunts (Schaller 1972; Van OrsdoI1984). The open and flat terrain at Etosha N.P. causes lionesses to be detected by prey before they are close enough to attack (see Elliot *et al.* 1977). Lionesses therefore hunt co-operatively by some lionesses rushing at the prey while others wait for the prey to run towards them (see Stander 1992a, b). As a result, larger groups increase the probability of success.

Third, during the eight-month-Iong dry season in Etosha N.P., a period of prey scarcity, solitary hunters did not meet the estimated minimum daily required food intake (Schaller 1972), and all females in groups acquired significantly more food (Stander 1992a). In contrast, groups of two to four lionesses in the Serengeti 'risked nutritional stress' during the periods of prey scarcity (Packer *et at.* 1990). The probability of hunting success in Etosha N.P. furthermore showed the strongest increase with group size in the dry season (Fig. 3).   ,

Fourth, individual lionesses in Etosha N.P. specialize in different hunting tactics by repeatedly occupying particular stalking roles, which has not been observed elsewhere in Africa (Scheel & Packer 1991). The probability of hunting success increased when all lionesses in a group hunted in their preferred positions (Stander 1992b).

A number of other variables have also been shown to affect hunting success in Etosha N.P. Different prides initially had a significant effect on hunting success which disappeared when a fifth variable (day/night) was added to the logistic model. Van Orsdol (1984) reported strong differences in the hunting success of different prides in Uganda, but did not consider possible covariations among variables. The best model (H, Table 1) for predicting hunting success by Etosha lions included the variables hunt class, lioness group size, prey species, day/night, terrain and the interaction between day/night and terrain.

Kills of vulnerable prey accounted for a relatively high success rate of non-co-ordinated group hunts (class A) and daytime hums in open terrain, such as the plains and saline pans. It is well known that ungulate neonates are vulnerable to predation (Lent 1974) and that'predators utilize such opportunities (Schaller 1972; Kruuk 1972; Van Orsdol 1984; Fitzgibbon 1990). Vulnerable prey are not an important component of the lion's diet in Etosha N.P. and the behaviour related to their capture is purely opportunistic.

When hunting large and fleet-footed prey, the most important food source, lions have the highest probability of success during moonless nights, when their probability of success is above 20% for most types of terrain, irrespective of cover. Several authors have suggested that sufficient vegetation cover is an important factor affecting hunting success, especially where lions hunt during the day (Schaller 1972; Elliot *et al.* 1977; Van OrsdoI1984). In the largely open habitat of Etosha N.P., hunting during moonless nights substitutes for the lack of cover. At Queen Elizabeth N.P., lions in two study areas were also more successful during moonless periods than when the moon was above the horizon (Van Orsdol1984).

During hunts of springbok and zebra, lions are more successful when the wind speed is high. Noise associated with high winds may decrease the prey's ability to detect a predator (Leuthold 1977) and therefore increase the probability of success. Because of low sample sizes these data are not corrected for wind direction, which has been shown to affect hunting success (Schaller 1972; Stander 1992a). Van Orsdol (1984) found some evidence of lions hunting more often when storms were approaching, but hunting success did not increase with wind speed. Wildebeest hunts in the present study, however, were less successful when wind speed was high. We have no explanation for this discrepancy other than differences in the anti-predatory behaviour of this species.

In the semi-arid environment of Etosha N.P., hunting success is greatly improved by co-operative hunting in large groups. The fundamental advantages of group hunting in securing large and fleet-footed prey in an open habitat (Wilson 1975) are reflected in the higher *per capita* food intake acquired by lionesses in groups during the long dry season. These results differ from studies in the Serengeti (Packer *et al.* 1990), an area of much higher prey density (East 1984), where groups do not achieve greater foraging success than solitary lions. The evolution of sociality in lions is complex (Packer 1986; Caro 1989), and recent advances have convincingly dismissed co-operative hunting as an evolutionary cause of sociality (Packer 1986) in cases where single prey are hunted and when individual hunting success is high (Packer & Ruttan 1988). However, the species lives at different densities throughout sub-Saharan Africa under varying ecological constraints (Sunquist & Sunquist 1989). In the harsh environmental

conditions of a semi-arid region such as Namibia, where individual hunting success is low, the social foraging habits of lions may have evolved in order to avoid nutritional stress. Understanding the differences in the behaviour of lions under contrasting ecological constraints may be crucial to the interpretation of the evolutionary causes of sociality.

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