

Group hunting behaviour of lions: a search for cooperation

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Abstract. The participation of individual African lions, *Panthera leo*, during 64 communal hunts of four prey species was measured to quantify the extent to which lions cooperate and the factors affecting the degree of cooperation. The extent of individual participation in communal hunts varied significantly. Finite mixture models were used to determine the probability that each lion's behaviour belonged to each of three strategies: 'refraining' (non-participation in hunts), 'conforming' (active participation in groups in which all individuals behaved similarly) and 'pursuing' (active participation in groups where individual behaviour varies). Our analysis reveals two important trends. First, males refrain more and pursue less than females. Second, refraining during a group hunt is more common during hunts of prey that appear to be easier to capture: lions are more likely to refrain during hunts of wart hog, *Phacochoerus aethiopicus*, and less likely to refrain during hunts of zebra, *Equus burchelli*, and buffalo, *Syncerus caffer*. Of the alternatives considered, the data indicate that refraining is 'cheating' and that lions exhibiting this strategy are thus exploiting the hunting behaviour of their companions. These results are discussed in the framework of a recent game-theoretical model of cooperative hunting.

Although foraging activities of African lions, *Panthera leo*, are widely and uncritically cited as examples of communal and highly cooperative hunting behaviour (e.g. Wilson 1975; Dorst & Dandelot 1983; Giraldeau 1984; Arms & Camp 1987; Alcock 1989), Schaller (1972, page 242) observed that one or more group members failed to join in the majority of hunts. In this paper, we confirm that pride-mates frequently do not participate to the same extent as their companions, and we test theoretical predictions of exploitation in socially foraging groups using a model of cooperative hunting (Packer & Ruttan 1988).

Individuals within a single foraging group may employ alternative strategies of food acquisition (e.g. Brockmann & Barnard 1979; Barnard 1984). 'Producer-scrounger' models of this phenomenon consist of two strategies where individuals either forage actively ('produce') or exploit the foraging behaviour of producers ('scrounge'; Dawkins 1980; Barnard & Sibly 1981; Sibly 1984). However, Packer & Ruttan (1988) modelled group hunting behaviour as a four-strategy game where individuals either (1) hunt actively, irrespective of the behaviour of companions ('cooperate'), (2) never hunt, but exploit any hunting behaviour of companions ('scavenge'), (3) hunt only under certain

circumstances, otherwise scavenge ('cheat') or (4) avoid conspecifics and always hunt alone ('solitary'). An individual that cheats hunts only if it spots the prey first and stops hunting if a companion starts to hunt. Thus, a cheater never hunts in the presence of a cooperator. In a group of two cheaters, each will hunt about half the time. Where individuals are constrained to live in groups, the strategy set is restricted to cooperate and cheat, because individuals cannot be solitary under these conditions and a strategy of pure scavenging is always replaced by cheating (Packer & Ruttan 1988).

Packer & Ruttan (1988) reviewed data from 28 studies of group hunting and showed that hunting success generally increases asymptotically with increasing group size in circumstances where individuals are expected to hunt cooperatively. Therefore, individuals that do not participate in group hunts withhold effort that would increase the group's success rate. Where non-participants are able to feed from a prey item captured by their hunting companions, they avoid any costs of prey capture and should therefore be viewed as cheaters.

Both theoretical approaches specify a wide range of conditions where only a small proportion of the

group will actively procure food items. However, producer–scrounger models focus on the stable coexistence of alternative strategies, whereas the models of Packer & Ruttan (1988) focus on conditions that affect whether individuals should cooperate or not. Traditional producer–scrounger models typically consider foraging for small, indivisible prey (kleptoparasitism; see Brockmann & Barnard 1979 for a review; Dawkins 1980) or prey that is small, numerous and not readily defensible (e.g. Barnard & Sibly 1981; Giraldeau & Lefebvre 1986). However, the models of Packer & Ruttan (1988) also include foraging for large, divisible prey, which is typical of social carnivores.

A large, divisible prey provides an opportunity for all group members (including non-participants) to feed. This appears to be true of typical lion prey: female pride-mates have equal access to carcasses (Packer & Pusey 1985); there is no social dominance among female lions in the same pride (Schaller 1972; Bertram 1978; Packer & Pusey 1985); and there is no significant variation in recent food intake (as measured by belly size) among female pride-mates (Pusey & Packer, unpublished data). Female lions appear to be constrained to live in groups by factors other than foraging efficiency (Packer et al. 1990) and we will focus much of our analysis on females, as they do almost all of the hunting when both sexes are present (Schaller 1972, page 242; also see Results).

Tests of Hypotheses

In this paper, we use the word ‘strategy’ only to specify behavioural types (*sensu* Maynard Smith 1982); we do not impute conscious decision-making by the animal.

For species that capture single, large prey (as is usually the case with lions), Packer & Ruttan’s (1988) models make four important predictions. First, the tendency to participate in prey capture is expected to increase with the difficulty of capturing a particular prey species. If the success rate of a lone hunter is very high, the participation of additional hunters can only improve capture rate slightly and thus the benefits of joining a hunt will be small relative to the costs. However, when success of a solitary hunter is very low, an additional hunter may improve the chances of capturing the prey sufficiently to overcome its own costs of participation. Indirect evidence supports this prediction in a number of species: the success of group hunting

generally does not increase with group size when the success rate of a single hunter is high, whereas group success increases rapidly when solo success rates are low (Packer & Ruttan 1988). In this paper, we provide the first direct evidence that this effect may be due to non-participation.

Second, poor hunters are expected to be less likely to participate than their more proficient companions, as the participation of an inept hunter will often have an insufficient effect on the success rate of the group to overcome its own costs of participation. Third, participation is expected to decline as the size of the hunting group increases. Group hunting success increases asymptotically with increasing group size (Packer & Ruttan 1988), and thus each additional animal’s effort makes a smaller contribution to the success of the hunt. Fourth, the genetic relationship of the hunting group members is expected to influence participation. It is a general feature of models of cooperation that greater kinship among group members leads to greater cooperation (e.g. Hamilton 1964; Boyd & Richerson 1988). In models of group hunting, closely related companions are expected to participate at higher levels of solo hunting success and at larger group sizes than unrelated companions (Packer & Ruttan 1988).

Inactivity during a group hunt might actually constitute cooperation if additional hunters would interfere with the hunt and lower the group’s success rate, or if inactive group members are really lying in wait to assist in catching prey that their more active companions drive toward them. In the first case, animals are expected to participate least when the risk of interference is highest. In the second, individuals that are inactive early in the hunt should often have an active role in capturing the prey late in the hunt.

In summary, we expect that an individual will be more likely to participate in a hunt (1) when the prey is difficult to capture, (2) when the individual is a relatively good hunter, and (3) when the group is small or (4) is composed of close relatives. We make two additional predictions: (1) if group members avoid interfering with companions by remaining inactive, then an animal will be more likely to pursue the prey actively when the risk of interference is low and (2) if group members hunt by division of labour, individuals that are inactive early in a hunt should often become active in the later stages of a hunt.

Identifying Behavioural Variation

To test these predictions, we developed a new method for analysing continuously distributed behavioural data. This method can reveal distinct strategies that are often obscured by the continuous nature of behavioural measurement.

For example, during a group hunt, each individual can decide either to pursue the prey or not. Individuals that pursue prey may travel varying distances before the hunt is terminated. However, individuals may also move toward the prey for reasons unrelated to prey capture (e.g. to remain with companions or to avoid being detected as non-participants). In addition, animals may follow other strategies such as 'conditional' and 'unconditional' hunter. Such strategies would exhibit different behaviour only under specific conditions.

Therefore, whatever the different behaviour patterns may be, we do not necessarily expect discrete, non-overlapping modes of activity. Instead, observed behaviour should often occur over a continuous range. Each strategy will contribute a component to this over-all distribution. The components may be identified from the observed distribution using finite mixture models (Dempster et al. 1977; Everitt & Hand 1981) that attempt to fit a mixture of two or more theoretical distributions to the observed behaviour. Each fitted component distribution is representative of one underlying strategy. Using this method, we show that lion behaviour during group hunts consistently varies among individuals within a pride: some lions actively participate during group hunts, whereas others remain inactive. This method of analysis may prove useful in other situations where the continuous nature of a behavioural variable obscures differences in individual strategies.

METHODS

Lions are the most social species of Felidae. Prides are social groups made up of one to 18 related adult females, their dependent offspring, and a coalition of one to nine adult males that has entered the group from elsewhere (Bygott et al. 1979; Packer et al. 1988). Lions in a 2000-km² area of Serengeti National Park, Tanzania, have been studied continuously since 1966, and this study group is currently made up of about 200 individuals (Packer et al. 1988).

Sampling Methods

Beginning in 1984, one female in each of 21 prides was fitted with a radio collar. Hunting activities of collared females and their companions were recorded during 96-h watches just before or after each full moon. Lions were located at the start of each 96-h watch using aerial radio-telemetry. 10 × 40 Zeiss binoculars were used for observations during the day; night observations were made using light intensifying goggles and 8 × 35 binoculars. Distances were measured using a Leitz range finder, the vehicle's odometer or estimated visually. Estimates were accurate to within 10%, based on trials where estimated distances were subsequently measured with the range finder and odometer. Lions were followed at the maximum distance permitted by light conditions to minimize disturbances to the lions and their potential prey. This was generally greater than 300 m during the day, and about 100 m at night. We observed 198 hunts during 3500 h of observation between September 1984 and December 1987. An additional 20 hunts were observed opportunistically in the same time period. A 'group' of lions was defined as all individuals of the same pride that were within 200 m of one another. Typically, however, all lions in a group began each hunt within 1–50 m of other group members.

To quantify participation of individuals during hunts, it is necessary to define a hunt broadly. This eliminates the need for arbitrary decisions about when a hunt starts or what constitutes a hunt, and ensures that hunts that failed early or that had very low levels of participation are included. Such hunts are of obvious importance in quantifying the frequency of participation. Throughout this paper, the terms 'hunt' and 'hunting' are used as follows. A group was considered to be hunting whenever at least one lion moved toward potential prey while exhibiting any of the following behaviour patterns (Schaller 1972, pp. 93–101, 240–248): alert face (oriented toward prey) combined with waiting in ambush, alert walk, stalking walk, crouching walk, crouch, trot, head-low trot or rush. Hunts are divided into two parts that are analysed separately: the 'stalk' includes any walking or crouching behaviour, the 'rush' includes trotting and rushing behaviour.

The three indicators we used to measure a lion's participation in a hunt were (1) the distance stalked toward the prey, (2) the time taken to cover that distance, and (3) whether the lion rushed the prey.

These are defined as follows: the approach distance is the total distance an individual stalked toward a potential prey, this does not include the rush. The approach duration is the total time a lion spent actively stalking toward the prey. Approach duration was more difficult to measure than distance because lions occasionally moved out of our view during a hunt. When an individual reappeared, it was possible to measure the distance it had travelled, but not to measure the amount of time the lion had been actively moving. Participation in a rush is defined as running or trotting toward the prey. Note that the measure of rush participation is independent of the distance and duration measures and is discrete rather than continuous.

Variation in available cover may alter the risk that individuals will interfere with one another during a hunt. Therefore, two characteristics of the environment were recorded for each hunt: habitat (long or short grass plains, open or dense woodland, riverine) and the type of cover available between lions and their prey (grass height, bushes, solid objects such as rocks, etc.). Data were also collected on how lions used cover (no cover, cover available but not used, cover used along a direct route to prey, lion went out of direct route to use cover, continuous cover).

Kinship among individuals could be assessed through the maternal line, although maternity could not be ascertained in some cases because of the communal rearing behaviour of females. Females within a pride usually give birth at about the same time and pool cubs of the same age to form a stable crèche (Packer & Pusey 1983; Packer et al. 1990). Where maternity was not known with certainty, the cub was at least known to belong to one of the females in the communal crèche. Therefore, we based our analysis of kinship on the probability that two individuals were first-order genetic relatives (e.g. mother–daughter, full siblings).

General Data Analysis

Lions hunted 17 different species during the study, but this analysis is restricted to hunts of wart hog, *Phacochoerus aethiopicus*, wildebeest, *Connochaetes taurinus*, zebra, *Equus burchelli*, and buffalo, *Syncerus caffer*. These species are the most important prey for the Serengeti lions in terms of frequency of hunts (130 of 218 hunts), the time involved in stalking (63.3 of 89.5 h), the number of kills (19 of 33), and the total food intake (1457 of 1640 kg acquired from predation). Prey availability

is highly seasonal in the Serengeti. Significant numbers of wildebeest and zebra are available in our study area only during the wet season (usually from November to January and from May to June; Schaller 1972; Maddock 1979; Packer et al. 1990). Wart hog and buffalo are non-migratory, and are critical prey when migratory herds are absent (Packer et al. 1990).

Except when otherwise stated, our analyses are based only on the behaviour of females (see above). Analyses of group hunts are based on hunts involving two or more lions greater than 2 years of age. Females appear to be competent hunters by that age (see below; also, Schaller 1972, pp. 153, 254), and at least two individuals must be present for cooperation to be possible. These criteria were fulfilled in 21 hunts of wart hog, 19 of wildebeest, 14 of zebra, nine of buffalo and one of a mixed herd of wildebeest and zebra. Analyses are based in these 64 hunts.

Rushes occurred on 22 hunts (34%) and analyses of rush participation include only those hunts where at least one lion rushed. Hunts without rushes do not provide information about the willingness of lions to rush, since many hunts end when prey are startled or move away before any lion has a chance to manoeuvre into a position where rushing might be productive.

Finite Mixture Models of Variation in Behaviour

Individual variability in hunting behaviour can be quantified by measuring the relative distances travelled and relative times spent engaged in a hunt. Data were scaled by dividing each individual's approach distance or duration by the average for all lions present during that hunt (e.g. if two lions travel 20 and 180 m respectively, the average length of the hunt is 100 m, and their scaled distances would be $20/100 = 0.2$ and $180/100 = 1.8$. If both travel 180 m, the scaled distance of each would be 1.0). Scaling controls for differences in the average lengths of hunts due to variation in the initial distance between lions and their chosen prey.

To examine the possibility of multiple strategies generating the observed distributions of behaviour, we attempted to fit well known theoretical distributions to the data sets. No single distribution gave an adequate fit, so finite mixture models of two or more distributions were tried (Dempster et al. 1977). The simplest model to fit any of the data sets was a mixture of three distributions (an exponential, normal and gamma). One strategy is inferred

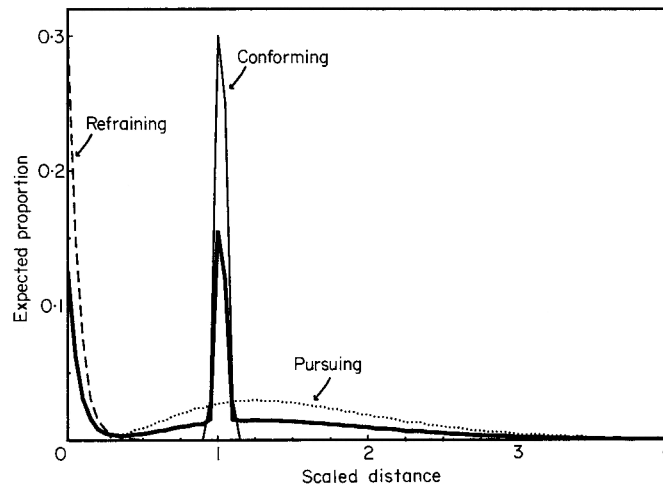


Figure 1. Component distributions of an idealized mixed distribution (heavy solid line). Each component (exponential, dashed line; gamma, dotted line; normal, light solid line) is representative of one behavioural alternative, as labelled. Scaled distance is the distance stalked by an individual, divided by the average distance stalked by all lions present during that hunt.

from each distribution necessary to approximate the complexity of the data; thus, our results imply three distinct strategies (see Fig. 1). The expected distribution based on this overall mixture model is referred to as the 'mixed distribution'. The mixed distributions were tested for significant differences from the data using a chi-squared goodness-of-fit test (Sokal & Rohlf 1981). Each data set was subdivided into the maximum number of cells for which the expected values would exceed five. Degrees of freedom were reduced according to the number of parameters used in estimating the mixed distribution (4: one for each component, plus a mixing parameter).

The choice of exponential, normal and gamma component distributions to form the mixed distribution is not meant to imply anything about the mechanisms that generate lion behaviour. These component distributions have the advantages of being well known and easy to work with. They were chosen for these reasons alone and not because the behavioural roles they infer were a priori expected to generate behaviour that would form these distributions. Therefore, no significance is attached to the use of any particular component distribution (e.g. a distribution other than an exponential might have been chosen to approximate the high frequency of non-participants without altering our results).

Rather than categorize an individual's behaviour as belonging to a particular strategy, the posterior

probability that a scaled distance (or duration) belonged to each component distribution was calculated (Dempster et al. 1977). A lion was thus assigned a probability of showing each of the three behaviour patterns, based on its scaled distance (an example of this for our data on wart hog hunts is presented in Table I). This method retains the continuous nature of the variation in the observed behaviour, and uses all available information. Our analysis of male behaviour is based on the distribution of female data points (i.e. a male is assigned the same probability of pursuing as is a female who has the same scaled approach distance or duration).

For the rush data, behaviour was discrete: any lion that rushed the prey was considered a participant, while any lion present but not rushing was counted as refraining. However, it should be noted that a lion may have 95% probability of pursuing based on distance or duration data without joining the final rush. Conversely, a lion could conceivably rush despite having a 95% probability of refraining during the stalk.

RESULTS

Variation in Hunting Behaviour among Female Pride Members

Our data clearly implied three distinct strategies. The first, 'refraining', is associated with an exponential component distribution that represents a

Table I. Probabilities assigned to scaled distances during wart hog hunts

Scaled distance	N	Probabilities		
		Refraining	Conforming	Pursuing
0	26	1	0	0
0.1	1	0.995	0	0.005
0.2	0	0.929	0	0.071
0.3	2	0.526	0	0.474
0.4	0	0.134	0	0.866
0.5	2	0.023	0	0.977
0.6	0	0.004	0	0.996
0.7	3	0.001	0	0.999
0.8	0	0	0	1
0.9	2	0	0.022	0.781
1.0	4	0	0.794	0.206
1.1	3	0	0.029	0.971
1.2	2	0	0	1
1.5	8	0	0	1
>1.5	17	0	0	1

A lion's scaled distance was the distance it travelled toward the prey, relative to the distances travelled by its companions during a hunt. Each lion was assigned a probability of showing each of the three strategies, according to the lion's scaled distance (see text for details). In this example, the probability that an individual was refraining was highest when its scaled distance was very close to zero. The probability of conforming was highest at scaled distances near 1.0. The probability of pursuing was highest at scaled distances both above and below 1.0.

high frequency of non-participants. This behaviour pattern consists of remaining immobile or stalking only a very short distance during a hunt. (For those individuals with a probability of refraining of greater than 0.5, the average (\pm SE) distance stalked was 1.1 ± 0.7 m, $N=80$.) The second, 'conforming' ($\bar{X} \pm \text{SE} = 631 \pm 116$ m, $N=41$), is represented by a normal distribution that results from frequent occurrences of scaled values near 1.0, where the probability of conforming is greater than 0.5. This behaviour pattern occurs on hunts where all lions behave similarly. Third, 'pursuing' is associated with a gamma component distribution that includes the remaining points ($\bar{X} \pm \text{SE} = 154 \pm 20$ m, $N=114$). This behaviour pattern consists of participating in a hunt, but to a greater or lesser extent than companions. The mixed distribution obtained from the finite mixture model was used to assign to each lion's behaviour a probability of belonging to each strategy (probabilities for scaled distances during wart hog hunts are given in Table I).

The data in Figs 2 and 3 show the scaled distances and durations for females during group hunts of

each prey species. The observed data clearly do not represent any simple distribution, and elements of each of the components of the mixed distribution are apparent. The mixed distribution does not deviate significantly from the observed data for any of the four distance data sets (Figs 2a, c and 3a, c). However, it does deviate significantly for three of the four duration data sets (Figs 2b, d and 3b, d). Results reported here are therefore based on approach distances and rush behaviour because the fit of the duration data is so poor. Duration results are included only for comparison.

Unequal participation of females in hunts was frequent, suggesting behavioural alternatives. Of 235 female approach distances, the mean probability of refraining was 0.33. A similar proportion of refraining was found for approach durations (0.33). In addition, 35% (31 of 88) of females present at the time of a hunt involving a rush at potential prey did not join the rush. Females that did not rush on such hunts showed a significantly higher probability of refraining during the stalk (Mann-Whitney U -test: $U=460.5$, $N_1=31$, $N_2=$

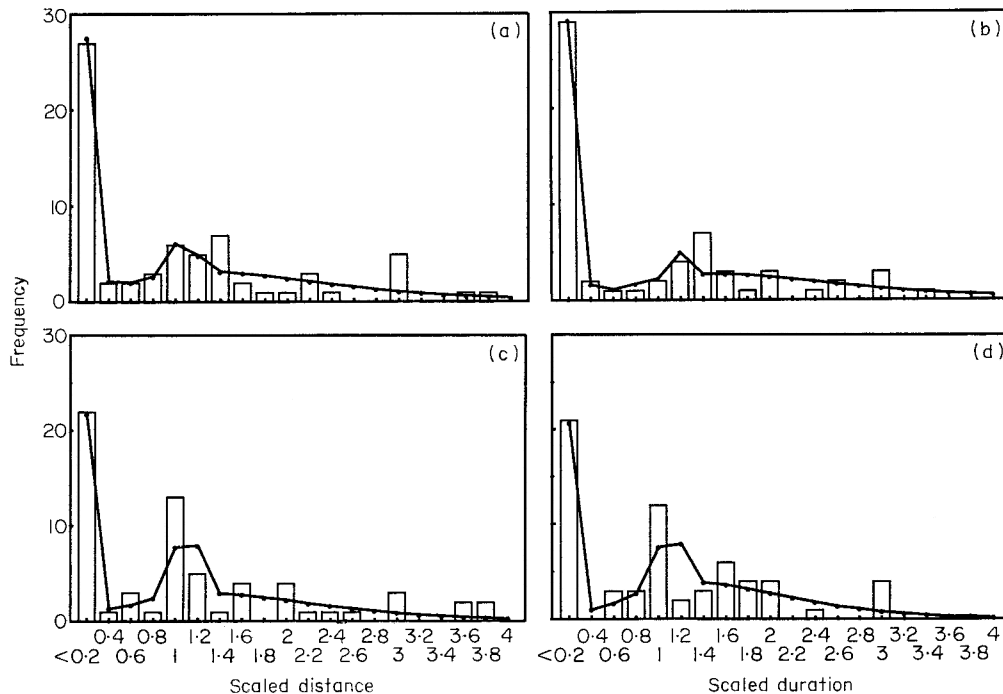


Figure 2. Bars indicate the frequency of each activity (scaled distance and scaled duration) of adult female lions during wart hog hunts (a and b) and wildebeest hunts (c and d). Lines indicate the mixed distribution fitted to each data set using finite mixture models. A mixture of three distributions was the minimum sufficient to approximate any of the observed data (chi-squared goodness-of-fit test, wart hog distance: $\chi^2 = 8.66$, $df = 4$, $P > 0.05$; duration: $\chi^2 = 12.19$, $df = 3$, $P < 0.01$; wildebeest distance: $\chi^2 = 6.41$, $df = 3$, $P > 0.05$; duration: $\chi^2 = 3.33$, $df = 3$, $P > 0.05$), implying three distinct behaviour patterns (see text for details).

57, $P < 0.001$), and a lower probability of pursuing (Mann-Whitney U -test: $U = 376.0$, $N_1 = 31$, $N_2 = 57$, $P < 0.001$) than females that did rush the prey. It is therefore clear that a significant portion of female lions frequently do not participate in a hunt.

In addition, individual lion behaviour frequently varied between hunts. Of 18 females observed hunting a particular prey species on two or more occasions, 12 (67%) showed high (> 0.5) probabilities of following different strategies during different hunts. Of four females that were repeatedly observed hunting two or more prey species, all four showed high probabilities of following different strategies during different hunts in at least one of these prey species. Two followed different strategies during different hunts of each respective prey species. Thus, the behaviour of most individuals varied across hunts, even when the same species was hunted (during hunts of wart hog, six of 10 females showed variable behaviour; wildebeest: five of nine females; zebra: six of six; buffalo: two of two).

The Effect of Species Hunted on Female Hunting Behaviour

To test Packer & Rutman's (1988) prediction that lions will be more likely to participate in a group hunt when the success rate of a single hunter is low, we contrasted the lions' hunting behaviour during hunts of species that varied considerably in body weight: wart hog (53 kg), wildebeest (170 kg), zebra (218 kg), and African buffalo (560 kg). The success rate with these prey is apparently related to the prey's size, although our sample size is limited (a total of 54 hunts by solitary lions with kills of four wart hog and two zebra). We improved our estimate of success rates by incorporating data from Schaller (1972) and restricting our analysis only to hunts in this study that meet Schaller's (1972) definition (the lion must approach to within 60 m of the prey). Solitary females hunting wart hog in this study are one and a half times as successful as those hunting wildebeest or zebra in Schaller's study (22%, $N = 18$ as opposed to 15%, $N = 33$). The success rate of solitary females is thus highest for

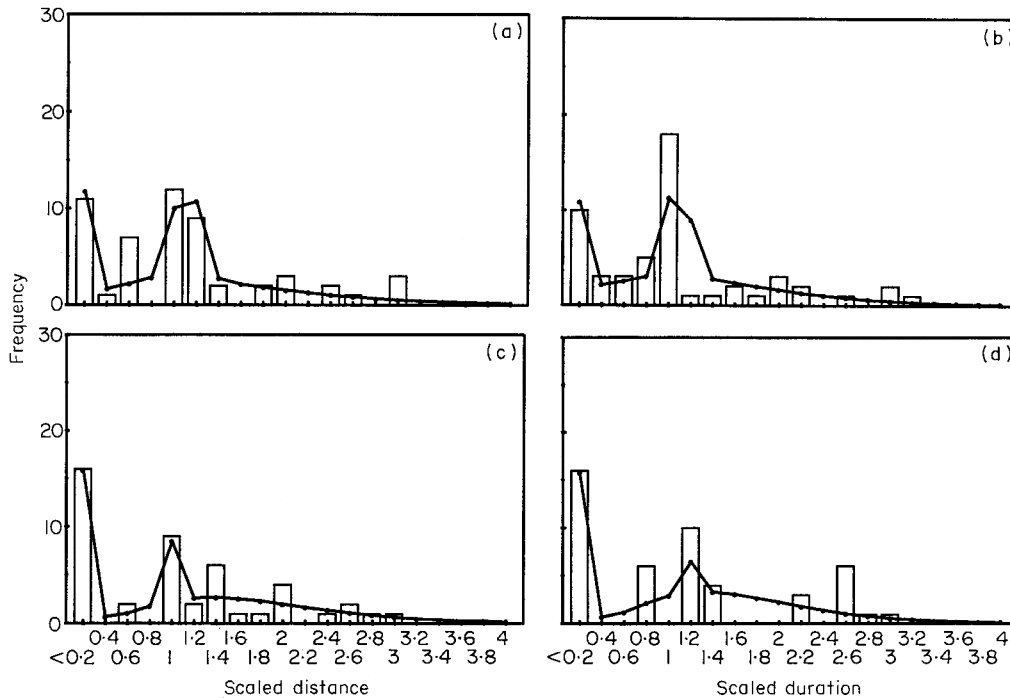


Figure 3. Activity of adult female lions during zebra (a and b) and buffalo (c and d) hunts. Details as in Fig. 2. Chi-squared goodness-of-fit test, zebra distance: $\chi^2=3.52$, $df=3$, $P>0.05$; duration: $\chi^2=6.18$, $df=2$, $P<0.05$; buffalo distance: $\chi^2=3.29$, $df=1$, $P>0.05$; duration: $\chi^2=13.25$, $df=1$, $P<0.001$.

wart hog, and lower for wildebeest and zebra (unfortunately, Schaller did not tally success rates separately for these two species). Finally, buffalo were never stalked by solitary lions in our study (presumably because a solitary's chance of success would be extremely low).

Female lions had a higher probability of refraining on communal hunts of wart hog than on hunts of zebra or buffalo (Fig. 4a; ANOVA, $df=3$, distance: $F=4.109$, $P=0.009$, duration: $F=2.548$, $P=0.062$). While females were equally likely to show pursuing behaviour across hunts of all four prey species (Fig. 4b; ANOVA, $df=3$, distance: $F=0.408$, $P=0.748$, duration: $F=1.942$, $P=0.130$), conforming was less frequent when wart hog was the intended prey (Fig. 4c; ANOVA, $df=3$, distance: $F=3.364$, $P=0.023$, duration: $F=3.848$, $P=0.013$). Note that even when levels of participation were highest, refraining was still common (mean probability of refraining on zebra hunts: 0.22; buffalo hunts: 0.34). We found no difference across species in the tendency of lions present to rush the prey (Fig. 4d; ANOVA, $df=3$, $F=0.097$,

$P=0.962$) nor in the tendency of individuals with a high (>0.5) probability of pursuing to rush the prey (ANOVA, $df=3$, $F=0.916$, $P=0.449$). However, when lions rushed toward the prey, it was impossible to distinguish those individuals genuinely intent on prey capture from those merely keeping close to companions to obtain a preferred feeding spot on the kill.

Variation in behaviour shown by lions at each hunt would be expected to affect the success rate of hunts. A comparison across all four species revealed that hunts resulting in a kill had a higher proportion of pursuing, and a lower proportion of refraining, than failed hunts. However, the sample size of successful hunts was small ($N=5$) and the differences were not significant. The proportion of conforming was nearly identical for successful and failed hunts.

The Effect of Age and Sex on Hunting Behaviour

Better hunters are expected to be more active than poor hunters during group hunts. Two variables that are likely to correlate with hunting

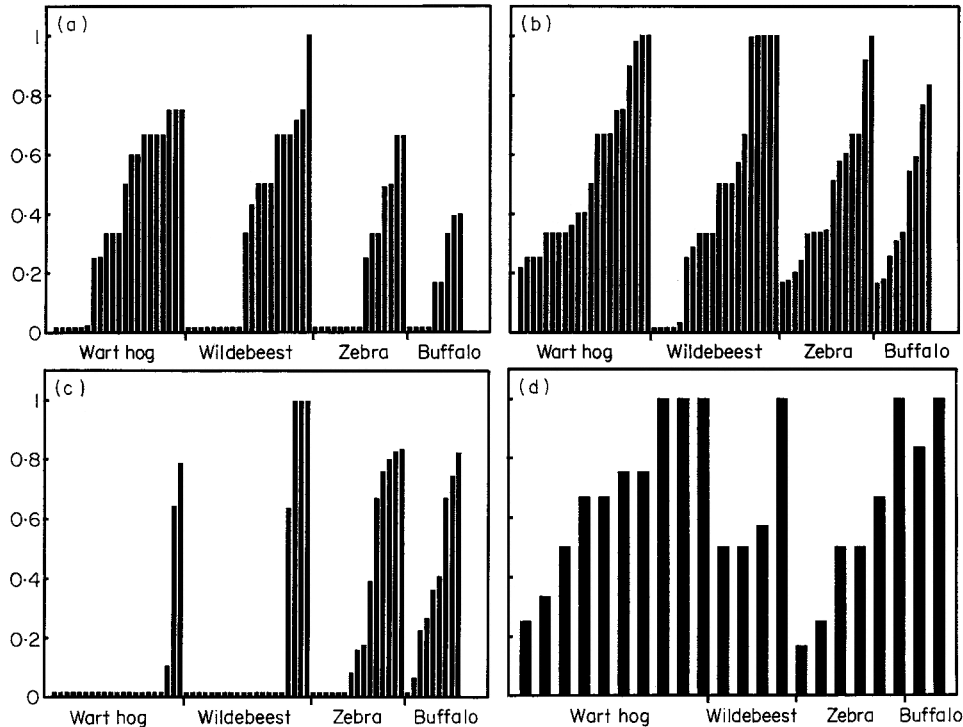


Figure 4. (a–c) Each bar represents the average probability of: (a) refraining, (b) pursuing and (c) conforming for all females in each hunting group on a single hunt. (d) Each bar represents the proportion of all females that participated in a rush at the prey. Hunts are grouped by prey species in order of increasing prey size. Refraining is more common during hunts of wart hog and less common during hunts of zebra and buffalo ($P=0.009$). Conforming is more frequent when refraining is rare (during hunts of zebra and buffalo; $P=0.023$). The P -values indicated are for differences between species (ANOVA, see text for details). There were no significant differences between species in pursuing or rushing behaviour.

proficiency are age and sex. While the age of hunting female lions in this study ranged from 2 to 14 years, we found no effect of age on any measure of hunting participation. However, there was a clear sex difference in hunting behaviour. Males had a higher probability of refraining than females (Fig. 5a; ANOVA, $df=1$, distance: $F=9.873$, $P=0.002$, duration: $F=6.074$, $P=0.016$) and a lower probability of pursuing (Fig. 5b; ANOVA, $df=1$, distance: $F=8.327$, $P=0.005$, duration: $F=7.567$, $P=0.007$). In addition, a lower proportion of males present joined rushes (Fig. 5d; ANOVA, $df=1$, $F=7.346$, $P=0.012$). There were no sex differences in the probability of conforming (Fig. 5c; ANOVA, $df=1$, distance: $F=1.433$, $P=0.235$, duration: $F=0.119$, $P=0.731$). These results applied to adult male hunting behaviour in the presence of females, and may not be representative of nomadic male behaviour.

Group Size and Kinship Versus Female Hunting Behaviour

We found that no measure of lion participation changed significantly with group size while hunting any of the four species. In addition, we found no effect of the average degree of maternal kinship on the probability that females pursued, refrained or conformed in a group hunt, when kinship was estimated either for the whole pride or only for those individuals present at the hunt. However, it should be noted that our estimates of kinship were coarse, and that after controlling for prey species our sample size may have been too small to detect either group size or kinship effects.

The Effects of Cover on Female Hunting Behaviour

The types of cover available to lions had no effect on any measure of participation in communal

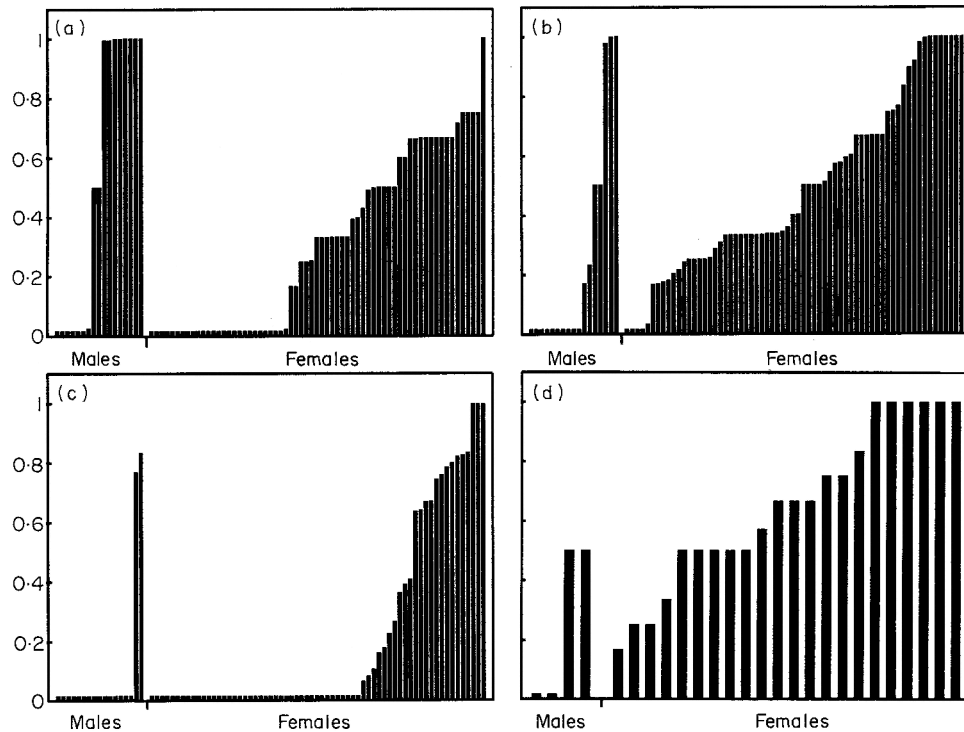


Figure 5. (a–c) Each bar represents the average probability of: (a) refraining, (b) pursuing and (c) conforming for all members of each sex present in the hunting group. (d) Each bar represents the proportion of each sex that participated in a rush at the prey. Hunts with both sexes present are therefore represented by one male and one female bar. Males refrain more ($P=0.002$), pursue less ($P=0.005$), and rush less ($P=0.012$) than females. The P -values indicated are for differences between sexes (ANOVA, see text for details). There were no significant differences between the sexes in the probability to conform.

hunting activities (MANOVA: $S=3$, $\theta=0.069$, $P=0.518$). However, the use of cover by lions did vary with activity in some circumstances. Lions always used any cover that was immediately adjacent to their route towards the prey. Among females taking an indirect route to use patchy cover, or hunting in continuous cover, each of the three hunting behaviour patterns occurred with nearly equal frequency. However, hunts occurring in areas lacking cover were associated with higher probabilities of pursuing, while lions using cover only along a direct route to the prey were more likely to be conforming (MANOVA: $S=3$, $\theta=0.123$, $P=0.029$). These patterns may be explained if lions fan out in the absence of cover, and if the use of cover only along a direct route to the prey constrains each lion to travel the same distance as companions that are also using cover along a direct route. We found no tendency for refraining to be affected by the cover use (ANOVA, exponential distribution: $F=0.266$, $df=3$, $P=0.849$). However, the analysis of cover use had to be

restricted to only those lions that moved towards the prey (33% of all female lions did not move at all), because it was not possible to measure a lion's use of cover if it did not move during a hunt. Note that all females were included for the analysis of cover availability.

DISCUSSION

We have used a continuous measure of hunt participation to test for distinct differences in the behaviour of individuals. The three component distributions fitted to this measure may be interpreted in a biologically plausible manner and allow an assessment of underlying behaviour: the exponential component and the gamma component are generated by refraining and pursuing during hunts in which lions show variability in behaviour, while the normal component is generated by conforming during hunts in which all lions show similar behaviour.

While the mixed distributions were successfully fitted to the distance data, they were significantly different from the duration data. However, duration may be an inappropriate measure of lion hunting effort for several reasons. Duration is more difficult to measure accurately than distance or rushing behaviour (see Methods). Lions may also adjust the time they take to traverse a given distance toward the prey to optimize their position relative to other hunters (e.g. a lion may take extra time to traverse a given distance to minimize the chance of engaging in the dangerous task of attacking the prey first). Thus, longer hunting durations may sometimes indicate that lions are less involved in hunting, rather than more. In addition, both approach distance and rush participation are necessarily correlated with energy expended upon hunting behaviour, while this may not be true of approach duration.

Success Rate and Relative Difficulty of Prey

Our data in combination with data from Schaller (1972) indicate that solitary hunters may have the highest success rates while hunting wart hog. Although Schaller (1972) did not tally success rates separately for wildebeest and zebra, zebra are slightly larger, and a zebra stallion's tactic of lagging toward the rear of a fleeing group and attacking an approaching predator makes the zebra a more dangerous prey (Kruuk 1972, pp. 181–184). Finally, buffalo are the largest of these four species and are capable of killing adult lions (Packer 1986). They present a serious challenge even to large prides. Solitary female success rates therefore appear to be inversely correlated with prey size. Refraining was most frequent during hunts of wart hog, the smallest prey, a pattern consistent with the predictions of Packer & Ruttan (1988). Note that although wart hog are relatively small, they are sufficiently large to feed all group members.

Age and Sex Effects

We found no effect of age on any of the three measures of hunting behaviour. However, we have no data on the effect of age on the success rate of hunts by female lions, and therefore do not know at what age young females become as proficient as adults. Male lions are far more conspicuous than females because of their large size (1.5 times as large as females, Smuts et al. 1980) and large manes, and

males may thus be poorer hunters than females, although there are no good data on the success rate of lone males. Males clearly contribute far less than females to communal hunts.

Is Refraining Really Cheating?

We have viewed refraining as behaviour that takes advantage of a companion's work at hunting. Other possible explanations for refraining and pursuing do not adequately explain the patterns of occurrence of these strategies. If lions cooperate by division of labour, with 'drivers' circling the prey, and 'catchers' lying in wait for their companions to chase the prey toward them, a similar pattern of refraining and pursuing might occur. However, if lions are driving and catching prey, then both lions that are pursuing and lions that are refraining are expected to participate equally in a final rush. Yet we found that those individuals rushing the prey are significantly more likely to be pursuing prior to the rush, and less likely to be refraining than are individuals that did not rush the prey. Hence, pursuing often involves active attempts to subdue prey, whereas refraining often involves letting pride-mates do the work.

Lions might also behave as 'pessimists' and 'optimists', where pessimists more sceptically evaluate the likelihood of success, and only participate in hunts that are likely to succeed. Such behaviour would clearly generate a pattern of pursuing and refraining. However, the observation that hunts of wart hog (the easiest prey) have the highest incidence of refraining indicates that this behaviour is not pessimism. A pessimist might assess that the high probability of success on a wart hog hunt makes it worth her effort to participate. In contrast, a cheater should not join such a hunt since her companions would be likely to succeed without her, and would do all the work.

Alternatively, all lions may participate in a hunt, but be forced to travel different distances by heterogeneity in cover or to avoid interfering with one another. The appearance of distinct strategies would then be an incidental consequence of constraints of the terrain. However, we found no effect of available cover on any measure of lion activity.

Conforming is an active strategy during hunts, and as such would be expected to be more similar to pursuing than to refraining. However, our data are insufficient to decide whether conforming could be a strategy such as conditional cooperation or concealed cheater. There is a tendency for conforming

probabilities to be high on long hunts. However, there is no significant tendency for a decrease in refraining as hunts get longer, indicating that conforming does not arise merely through a tendency of lions to remain close to their companions. While the sample size of kills is small ($N = 5$, all species), both conforming and pursuing occurred more frequently on hunts that resulted in kills than on hunts that did not, whereas the reverse was true of refraining. However, conforming and refraining both occurred more frequently on hunts without rushes than on hunts with rushes; while the reverse was true for pursuing. Conforming therefore appears to be behaviourally distinct from both refraining (cheating) and pursuing (cooperating), although the functional significance of this strategy is unclear.

Cheating, therefore, appears to be common among lions and is not restricted just to males. Are the same individuals prone to cheat in every hunt, while others do the work? Most individuals clearly assume different roles in different hunts. However, even after 3500 h of observations we saw insufficient hunts by any one group to determine whether some individuals show a statistical tendency to specialize. While cheating is common among lions during communal hunts, cooperation is at least as common during hunts of these four species. Cooperation is most common during hunts of larger and more difficult prey.

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REFERENCES

- Alcock, J. 1989. *Animal Behavior: an Evolutionary Approach*. 4th edn. Sunderland, Massachusetts: Sinauer.
- Arms, K. & Camp, P. S. 1987. *Biology*. 3rd edn. Chicago: Saunders College Publishing.
- Barnard, C. J. 1984. The evolution of food-scrounging strategies within and between species. In: *Producers and Scroungers: Strategies of Exploitation and Parasitism* (Ed. by C. J. Barnard), pp. 95–126. New York: Chapman & Hall.
- Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers: a general model and its application to feeding flocks of house sparrows. *Anim. Behav.*, **29**, 543–550.
- Bertram, B. C. R. 1978. *Pride of Lions*. New York: Charles Scribner's Sons.
- Boyd, R. & Richerson, P. 1988. The evolution of social behavior in sizeable groups. *J. theor. Biol.*, **132**, 337–356.
- Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. *Anim. Behav.*, **27**, 487–514.
- Bygott, J. D., Bertram, B. C. & Hanby, J. P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature, Lond.*, **282**, 839–841.
- Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? In: *Sociobiology: Beyond Nature/Nurture?* (Ed. by G. W. Barlow & J. Silverberg), pp. 331–367. Boulder, Colorado: Westview Press.
- Dempster, A. P., Laird, N. M. & Rubin, D. B. 1977. Maximum likelihood from incomplete data via the EM algorithm. *J. R. Stat. Soc. B*, **39**, 1–38.
- Dorst, J. & Dandelot, P. 1983. *A Field Guide to the Larger Mammals of Africa*. London: Collins.
- Everitt, B. & Hand, D. J. 1981. *Finite Mixture Distributions. Monographs on Applied Probability and Statistics*. New York: Chapman & Hall.
- Giraldeau, L.-A. 1984. Group foraging: the skill pool effect and frequency-dependent learning. *Am. Nat.*, **124**, 72–79.
- Giraldeau, L.-A. & Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim. Behav.*, **34**, 797–803.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. *J. theor. Biol.*, **7**, 1–16.
- Kruuk, H. 1972. *The Spotted Hyena: a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.
- Maddock, L. 1979. The 'migration' and grazing succession. In: *Serengeti: Dynamics of an Ecosystem* (Ed. by A. R. E. Sinclair & M. Norton-Griffiths), pp. 104–129. Chicago: University of Chicago Press.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. New York: Cambridge University Press.
- Packer, C. 1986. The ecology of sociality in Felids. In: *Ecological Aspects of Social Evolution: Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 429–451. Princeton, New Jersey: Princeton University Press.
- Packer, C., Herbst, L., Pusey, A. E., Bygott, D., Hanby, J. P., Cairns, S. J. & Borgerhoff Mulder, M. 1988. Reproductive success of lions. In: *Reproductive Success:*

- Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T. H. Clutton-Brock), pp. 363–383. Chicago: University of Chicago Press.
- Packer, C. & Pusey, A. E. 1983. Adaptations of female lions to infanticide by incoming males. *Am. Nat.*, **121**, 716–728.
- Packer, C. & Pusey, A. E. 1985. Asymmetric contests in social mammals: respect, manipulation and age-specific aspects. In: *Evolution: Essays in Honour of John Maynard Smith* (Ed. by P. J. Greenwood, P. H. Harvey & M. Slatkin), pp. 173–186. Cambridge: Cambridge University Press.
- Packer, C. & Rutten, L. 1988. The evolution of cooperative hunting. *Am. Nat.*, **132**, 159–198.
- Packer, C., Scheel, D. & Pusey, A. E. 1990. Why lions form groups: food is not enough. *Am. Nat.*, **136**, 1–19.
- Schaller, G. B. 1972. *The Serengeti Lion: a Study of Predator Prey Relations*. Chicago: University of Chicago Press.
- Sibly, R. 1984. Models of producer/scrounger relationships between and within species. In: *Producers and Scroungers: Strategies of Exploitation and Parasitism* (Ed. by C. J. Barnard), pp. 267–287. New York: Chapman & Hall.
- Smuts, G. L., Robinson, G. A. & Whyte, I. J. 1980. Comparative growth of wild male and female lions (*Panthera leo*). *J. Zool., Lond.*, **190**, 365–373.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry: the Principles and Practice of Statistics in Biological Research*. 2nd edn. New York: W. H. Freeman.
- Wilson, E. O. 1975. *Sociobiology: the New Synthesis*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.