Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*

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Abstract. Theoretical and experimental studies of assessment in animal contests have, until now, focused on disputes between single individuals. However, whereas single competitors usually avoid fights with opponents that are larger or stronger than themselves, in contests between social groups competitors might be expected to adjust their agonistic behaviour according to the number of individuals in their own and the opposing group. This hypothesis was tested using playback experiments to generate controlled artificial contests between groups of female lions. Recordings of single females roaring and groups of three females roaring in chorus were played back to simulate the presence of unfamiliar intruders within the territories of 21 different lion prides in Serengeti National Park, Tanzania. Defending adult females were less likely to approach playbacks of three intruders than of a single intruder and on occasions when they did approach three intruders they made their approach more cautiously. Defenders also carefully adjusted their decision to approach according to the size and composition of their own group, and attempted to recruit extra companions to the contest by roaring when some were absent at the time of playback. A strong selective advantage to avoiding the costs of fighting with larger groups could have led to the widespread evolution of numerical assessment skills in social species.

Animal contests over the possession of resources are usually asymmetric (Parker 1974; Maynard Smith & Parker 1976; Hammerstein 1981; Maynard Smith 1982). Apart from asymmetries in resource ownership that are sometimes used to settle contests at their outset (Davies 1978; Packer & Pusey 1982), and in the value of the resource to each opponent (Austad 1983; Enquist & Leimar 1987), opponents differ in their ability to acquire or defend resources (resource-holding potential: Riechert 1978 after Parker 1974, see Sigurjonsdottir & Parker 1981). Game theoretical models predict that where fighting is costly, contestants should assess the value of the resource and the resource-holding potential of their opponent, and withdraw without escalation if they would be unlikely to win an ensuing fight (Parker 1974; Maynard Smith 1982; Enquist & Leimar 1983, 1987).

Theoretical and experimental studies of assessment in animal contests have focused exclusively on disputes between single individuals (e.g. Davies & Halliday 1978; Clutton-Brock & Albon 1979; Maynard Smith 1982; Enquist & Leimar 1983; Robertson 1986). However, whereas single competitors usually avoid committing themselves to serious fights with opponents that are larger or stronger than themselves (Davies & Halliday 1978; Clutton-Brock et al. 1979; Robinson 1985; Robertson 1986; Rosenberg & Enquist 1991), in contests between social groups efficient assessors should consider the number of individuals that they can expect to encounter in a direct interaction. In social mammals, for example, where group members often co-operate to defend shared resources and large groups tend to dominate smaller ones in inter-group encounters (Harrington & Mech 1979; Cheney 1986; Packer et al. 1990), competitors might be expected to assess their opponents on the basis of characteristics that indicate relative group size.

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Lions are the only felids in which females, as well as males, are social (Schaller 1972; Packer et al. 1988). Whereas male lions form coalitions to compete for access to female groups (Bygott et al. 1979; Packer et al. 1988), female sociality may have multiple causes including benefits to be derived from group defence of territories and young (Packer et al. 1990). Up to 18 adult females and their dependent offspring live in close knit social groups known as prides and advertise their joint ownership of a territory by scent marking and roaring. Inter-pride encounters sometimes result in intense chases which are more likely to be won by the larger group of females (Packer et al. 1990), but fighting entails a high risk of serious injury and is rarely observed.

Evolutionary game theory would predict that female lions faced with a potential direct encounter with another pride should assess the likely outcome of a contest and commit themselves to chases or fights only in situations where they are likely to win. If female lions assess opponents on the basis of group size, they should adjust their agonistic behaviour in contests according to the number of individuals in their own and in the opposing group. We tested this hypothesis experimentally in a free-ranging population of lions in Serengeti National Park, Tanzania. Controlled artificial contests were generated by simulating the presence of intruders in pride territories with playbacks of unfamiliar females roaring.

METHODS

Study Population

All lions involved in this study belonged to a population of around 200 known individuals in a 2000-km^2 area of Serengeti National Park, Tanzania. Study animals were individually recognizable from natural markings (Packer et al. 1988). Demographic records have been maintained continuously on the population since 1974 (Bygott et al. 1979; Packer et al. 1988) and records on two prides date back to 1966 (Schaller 1972). The playback experiments described in this paper were conducted between January 1989 and July 1991.

Playback Experiments

Controlling the number of intruders and defenders

Female lions deliver their roars in bouts which generally last less than a minute and consist of

several soft introductory moans, a series of full throated roars and a terminating sequence of grunts. When pride members roar together the bout is delivered in chorus, one individual initiating and others joining in as the bout progresses by adding their roars in an overlapping fashion. We set the number of intruders at either one or three by playing back recordings of seven different females roaring alone and of four different choruses of three females roaring together. Two of the choruses were naturally occurring choruses and two were generated artificially using conventional sound mixing techniques (McComb 1992). Playback tapes were constructed so that the same individual females presented roaring alone in playbacks of a single intruder could also be presented roaring in chorus in playbacks of three intruders (McComb 1992). Under these circumstances any difference in response to a single versus three intruders is unlikely to be due to particular phenotypic characteristics of the individuals presented as single callers (but see also Results for further analysis of the effect of recording sequence on response). In all cases the subjects were unfamiliar with the females whose roars were used in playbacks.

The number of defenders in contest situations was varied systematically by playing back to female subjects in groups of different sizes.

Protocol

Natural encounters between Serengeti prides occur on average once every 5 days and usually take place during the hours of darkness and half-light (Packer et al. 1990). Roaring is also generally restricted to this period and prides roar relatively infrequently, females on the Serengeti plains averaging only 0·27 roaring bouts per h even at times when roaring rates are at their maximum (Hanby et al., in press). The protocol followed in our experiments was designed both to simulate the natural circumstances for roaring and inter-pride encounters, and to avoid habituating the subjects to playback.

Playbacks to the same groups of females were always separated by at least 7 days and were restricted to situations where the females were in a central part of their territory, had no adult males present with them and were not feeding. A single bout of roaring lasting 25–55 s (see above) was played 30 min prior to dusk using a Panasonic SV-250 Digital Audio Tape Recorder, an ADS P120 amplifier and a Klipsch Heresy Speaker placed at 200 m

from the subjects (as measured on a Land Rover odometer), and repeated once after 5 min if the subjects had not moved. Available vegetation was used to conceal the loudspeaker, which was connected to the tape recorder and amplifier (operated from within a Land Rover) by 100 m of cable. The playback system produced a peak sound pressure level of 116 dB at 1 m which was comparable in loudness to natural lion roars (a single roarer produces a sound pressure level of around 114 dB at 1 m). Responses of subjects were monitored for 1 h from the onset of playback using a Sony CCD-F40 8 mm video camera and field notes. After sunset, observations were made with the aid of night vision equipment.

Criteria used to document responses to playback

In response to playback, female lions either remained in their original position looking intently in the direction of playback, retreated in the opposite direction or approached the loudspeaker. In an approach they stood up and walked tensely towards the speaker with their heads low, usually punctuating their approaches with pauses and sometimes turning their heads to monitor the positions of companions during the approach. Whether or not the subjects approached the loudspeaker, the median latency in seconds between the onset of playback and adult female defenders in the group passing the loudspeaker (latency to speaker) and the number of times the lead subject paused or looked at a companion on the way to the loudspeaker were taken as indicators of the readiness of the defenders to engage in a contest with the intruders.

Hypothesis testing

If female lions assess the likely outcome of contests on the basis of the number of individuals in their own and in the opposing group, they should be more reluctant to approach playback when their own group size is small and/or when the opposing group is large. We tested this in three ways.
(1) Tightly controlled pairs of playbacks where the same adult females in each of 10 different prides were played on separate occasions recordings of single intruders and three intruders roaring. This allowed the effect of number of intruders on response to be examined while number (and identity) of defenders was held constant experimentally.

(2) Playbacks of single intruders to subjects in each of 18 different prides with group sizes ranging from one to six adult females. Here the effect of number of defenders on response could be examined while holding number of intruders constant experimentally.
(3) A total of 41 playbacks of one or three intruders to 21 different prides. Here the following varied across playbacks: (a) number of intruders; (b) number of defenders; (c) average age of adult females in the defending group (mean female age); (d) total number of adult females that belonged to the pride, the full quota of which were not necessarily present at the time of playback (maximum pride size); (e) number of immature offspring between 1 and 3 years of age present with the pride (number of subadults); (f) whether or not cubs were present.

Using multivariate statistics (see below) the relative effects of each of the above variables on female responses could be partitioned out, allowing an evaluation of a wider range of asymmetries that are common in real contests between female groups. In the same analysis we tested for confounding effects of pride identity and recording sequence played on female responses.

The effect of each of the independent variables on the willingness of subjects to approach the loudspeaker was tested at two levels: (1) whether or not they approached and (2) how cautiously they approached in situations in which an approach was made.

Log-linear analysis, a form of generalized linear modelling available in GENSTAT (Alvey et al. 1982; Payne et al. 1987), was used to examine the effect of each independent variable on the binary dependent variable approach = 1, no approach = 0 (see Fig. 1 and Table III for further details of the methodology, and Albon et al. 1986 for application of the technique to a comparable problem). For playbacks in which subjects approached the loudspeaker, the effect of each of the same variables on latency to speaker, number of pauses and number of looks at companions was examined using analysis of variance techniques. As the amount of vegetation cover available to conceal the simulated intruders might have had a confounding effect on how cautiously subjects approached the loudspeaker, we also tested for an effect of this variable (scored on a scale of 0–4) on all parameters of the approach.
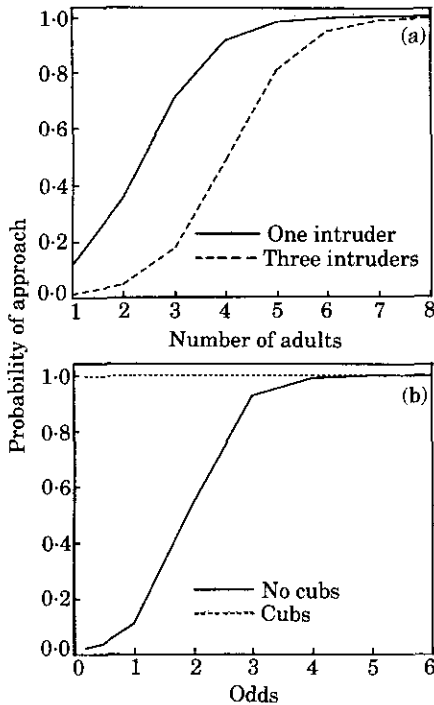
Figure 1. Logistic curves fitted to the probability of an approach occurring using models of the form:

$$P(Y_i = 1) = \frac{\exp(A + B_1 x_{i1} + B_2 x_{i2} + B_3 x_{i3} + B_4 x_{i4})}{1 + \exp(A + B_1 x_{i1} + B_2 x_{i2} + B_3 x_{i3} + B_4 x_{i4})}$$

(a) one to eight adult females faced with one and three intruders where x_{i1} = number of adult females; x_{i2} = number of subadults; x_{i3} = absence of cubs (0 = cubs present, 1 = cubs absent); x_{i4} = intruders (0 = 3 intruders, 1 = 1 intruder); i = 1 to 41; constants: $A = 3\cdot40$, $B_1 = 1\cdot49$, $B_2 = 2\cdot81$, $B_3 = -9\cdot4$, $B_4 = 2\cdot43$ and number of subadults and absence of cubs are set at their median values of 0 and 1, respectively. (b) Odds of $0\cdot2$–6 facing groups with and without cubs where x_{i1} = odds; x_{i2} = number of subadults; x_{i3} = absence of cubs (0 = cubs present, 1 = cubs absent); i = 1 to 41; constants: $A = 4\cdot76$, $B_1 = 2\cdot33$, $B_2 = 2\cdot66$, $B_3 = -9\cdot22$, and number of subadults is set at its median value of 0.

RESULTS

Effect of Number of Intruders

The number of intruders played from the loudspeaker affected how willing the defenders were to approach. In paired tests where subjects were presented with playbacks of a single intruder roaring and three intruders roaring together, they were consistently more reluctant to approach three intruders (Table I; sign test: $x = 0$, $N = 9$, $P = 0\cdot004$, two-tailed). In playbacks where subjects

Table I. Results of paired playback experiments where the same females were played on one occasion three intruders and on another occasion one intruder roaring from the loudspeaker

Pride (no. females)	Intruders	
	3	1
Transect (3)*	2041 (11, 2)	248 (2, 0)
Plains (4)*	2471 (28, 9)	292 (0, 0)
Barafu (3)	1525 (43, 16)	477 (10, 7)
Simba (2)*	511 (4, 4)	439 (4, 2)
Gol United (2)*	726 (7, 4)	258 (0, 0)
Campsite III (1)	707 (13, 7)	289 (4, 2)
Gol East (3)	Stay	371 (6, 2)
Sametu (3)	Stay	574 (15, 2)
SBG (1)	Retreat	Stay
BME (1)	Stay	Stay

Median latency to the speaker (s) of defenders and, (in parentheses), number of pauses and number of looks, respectively, are shown.
*Indicates situations where there was more than one potential leader present and yet the same individual led the pride to the loudspeaker in both playbacks of the pair; the probability of obtaining this result by chance for the combination of pride sizes shown above is $0\cdot0139$ (note that the comparison is only possible in situations where prides containing more than one female approach both three intruders and a single intruder).

approached both sets of intruders, when approaching three intruders they were slower to reach the loudspeaker (Wilcoxon matched-pairs signed-ranks test: $T^+ = 21$, $N = 6$, $P = 0\cdot032$, two-tailed) and they looked around at their companions more often (Wilcoxon: $T^+ = 21$, $N = 6$, $P = 0\cdot032$, two-tailed) than when approaching a single intruder. There was also a tendency (which bordered on statistical significance) for subjects to pause more often when approaching three intruders (Wilcoxon: $T^+ = 15$, $N = 5$, $P = 0\cdot062$, two-tailed).

It was notable that particular individuals adopted the role of leader in paired playbacks to the same pride. In four out of the five cases where prides containing more than one adult female (and thus more than one potential leader) approached each of three intruders and one intruder roaring, the same individual led the pride to the loudspeaker on both playbacks of the pair (Table I).

Effect of Number of Defenders

The number of adult female subjects in the defending group affected the likelihood that they

Table II. Results of playing back a single intruder to each of 18 different prides

Group size	Approach	No approach
< 3 (range = 1–2)	5	5
≥ 3 (range = 3–6)	8	0

Table III. Results of log-linear analysis to determine parameters affecting the binary variable approach = 1, no approach = 0

Variable	χ^2	df	P
No. defending adult females	8·39	1	<0·01
No. intruders	3·86	1	<0·05
No. subadults	13·64	1	<0·001
Presence of cubs	12·21	1	<0·001
Mean female age	0·14	1	NS
Maximum pride size	3·50	1	NS
Pride	21·82	20	NS
Recording	3·58	10	NS

The deviance value of a model when it includes a particular set of parameters provides an index of its goodness of fit. Whether inclusion of extra parameters in the model significantly improves the fit can be tested by comparing the difference between the deviance values of any two models, which are distributed approximately as chi-squared (χ^2), with degrees of freedom (*df*) equivalent to the difference in the number of parameters fitted in each model (Albon et al. 1986). The chi-squared values listed show the deviance attributed to each of the parameters when dropped from the model which included the maximum number of significant variables.

would approach playbacks of a single intruder. Single females and females in groups of two were significantly less likely to approach the loudspeaker than females in groups of three or more (Table II; Fisher's exact probability test: $N=18$, $P=0·0294$).

Partitioning out Contest Asymmetries

Log-linear analysis

Number of defending adult females, number of intruders, number of subadults and presence of cubs, all had significant effects on the probability of approach (Table III). A logistic model accounting for 59·4% of the deviance in probability

of approach showed that, as before, likelihood of approach increased with number of defending adult females and decreased with increasing number of intruders (Fig. 1a). Furthermore, subjects were more likely to approach the loudspeaker with increasing numbers of subadults, and when they had cubs. Number of defending adult females and number of intruders could also be replaced with the single variable 'odds', calculated as the ratio of number of defenders to number of intruders, to produce an equivalent model explaining 60·4% of the deviance in probability of approach. Adult female defenders without dependent offspring preferred odds of 2:1 before approaching, while those with cubs were considerably more likely to approach (Fig. 1b).

Analysis of variance

In 26 out of 41 playbacks that resulted in approaches, analysis of variance revealed that only one variable, number of intruders, affected all of latency to speaker, number of pauses and number of looks (Table IV). Females were more cautious of approaching three intruders than one intruder and this was irrespective of the number of females in their own group. Age affected latency to speaker (but not number of pauses and number of looks), defenders with a higher mean age taking longer to approach. This may have been partly the result of very old females (16 years and over) lagging at the back of the defending group. Finally, presence of cubs affected number of pauses (but not latency to speaker or number of looks), subjects with cubs pausing less often than those without.

In both analyses, neither pride nor recording sequence had an effect on the dependent variable, so that separate playbacks to the same pride and separate playbacks of the same recording sequence could be considered independent without pseudo-replication (McGregor et al. 1992).

Roaring in Response to Playbacks

Roaring after playbacks appeared to be a signal to absent pridemates rather than to the intruders themselves. Females rarely roared in response to playbacks, but were significantly more likely to roar when the number of defending adult females was less than the maximum pride size (Table V; $G=9·55$, $P<0·01$). Additional females joined the subjects at the playback site in 43% of these cases.

Table IV. Results of ANOVA on latency to speaker, number of pauses and number of looks for playbacks in which females approached the loudspeaker

Approach parameter	Variance components	% Variance explained	F	df	P
Latency to speaker	Number of intruders and mean female age	35·0	12·92	1,23	<0·005
			6·63	1,23	<0·025
Number of pauses	Number of intruders and presence of cubs	34·4	10·24	1,22	<0·005
			6·16	1,22	<0·025
Number of looks	Number of intruders	25·1	8·36	1,21	<0·01

Table V. Roaring after playbacks

Group size	Roared	Did not roar
Maximum	1	26
Less than maximum	7	7

DISCUSSION

While in naturally occurring contests visual and olfactory signals would sometimes also provide information on the intruders, in our experiments subjects were able to assess the number of opponents that they faced simply by listening to their roars. Not only were subjects less likely to approach playbacks of three intruders than of a single intruder, but when they did approach three intruders they undertook the approach more cautiously. As lions roaring in chorus overlap their roars, a single lion is incapable of producing a sound equivalent to a group of three. Because of this constraint, roaring choruses provide an honest advertisement that more than one individual is present in the group. The same should be true of other social mammals where group members overlap each other's calls in choruses (e.g. Harrington & Mech 1979; Sekulic 1982; Raemaekers & Raemaekers 1984; East & Hofer 1991). Constraints of this sort could provide a route to honest signalling that is distinct from the development of signals that are energetically very costly to produce (cf. Zahavi 1991).

Although roaring choruses provide a reliable indication of the number of individuals present for group sizes of three and less, the accuracy with which group size can be assessed may well decrease as chorus size increases substantially above this.

There is an upper limit in the ability of listeners to discern different individuals calling set by the auditory processing system (Miller 1956), and large numbers of individuals calling together in an overlapping fashion can sound confusing (see Harrington 1989). Harrington (1989) suggested that chorus structure in wolves, *Canis lupus*, has evolved to give an inflated impression of the number of individuals present in the pack, but did not test this experimentally. We would predict that in wolves and other social mammals where group members vocalize together, assessors should use chorused vocalizations as an indicator that more than one individual is present in a group, but only as an approximate cue to group size once chorus size exceeds two or three.

Defending female lions also carefully adjusted their agonistic behaviour according to their own group size, and the ratio of their own group size to that of the intruders (odds) was a good predictor of whether or not they would approach. Given that the asymmetry of territory ownership was always in their favour, females without cubs or subadults required high odds (usually 2 to 1) to approach the roars of intruders. It may be that defenders were compensating for the possibility that the number of intruders in the territory could have exceeded the number of individuals that they could hear roaring, or that the benefits of reinforcing territory ownership for females with no dependent offspring do not greatly outweigh the high costs of fighting (see below).

Parallel work, in which coalitions of adult male lions were played recordings of strange males roaring (Grinnell et al., in press), shows that resident male defenders must be outnumbered by 1 to 3 before their probability of approaching the simulated intruders is even marginally reduced. The difference between the responses of adult

females and resident males to playbacks of like-sexed opponents probably stems from the different proportions of their reproductive success that are at stake if a challenge is ignored. Matrilines of female lions hold long-term territories and territorial boundaries are slow to shift (Packer et al. 1988). Consequently, females that have no dependent offspring may lose relatively little by failing to reinforce territorial ownership in response to a single instance of intrusion by females that are unfamiliar to them. In contrast, male coalitions are resident in a pride for only 2–3 years and those that are evicted from their pride by incoming coalitions rarely gain residence in another (Packer et al. 1988). If in failing to respond to a challenge by strange males residents lose their females to another co-alition, they could stand to forfeit their entire lifetime reproductive success. These are just the conditions under which theoretical models predict the evolution of fatal fighting (Enquist & Leimar 1990).

The probability that female defenders would approach a set number of intruders increased dramatically when cubs were present. The most likely explanation for the over-riding effect of cubs on probability of approach is that the value of the territory to the pride becomes substantially greater while they are rearing young (Packer et al. 1990; see also Enquist & Leimar 1987) and that females with cubs, like resident male lions, stand to lose a substantial proportion of their reproductive success by ignoring a challenge. An alternative explanation is that there is a greater cost to ignoring a challenge when cubs are present because they are particularly vulnerable to surprise attacks from the intruders. However, females often abandon the cubs during their approach to the loudspeaker and in doing so appear to put them at an even greater risk. This contrasts with their behaviour after playbacks of unfamiliar, potentially infanticidal males which is markedly oriented towards cubs (McComb et al. 1993).

Probability of approach by female defenders also increased with increasing numbers of subadults. This may have been at least partly because subadults, as dependent offspring, increased the relative value of the territory to the pride or were susceptible to attack. A third possibility, however, is that subadults, although smaller and less experienced than adult females, represent extra defenders that might participate in an ensuing chase or fight.

Although subjects did not adjust their decision to approach the intruders or the caution with which they approached according to their own maximum pride size, there was evidence that they attempted to recruit absent pride-mates to the contest by roaring. Their roaring was largely confined to situations where at least one adult female pride member was absent from the group at the time of the experiment and on nearly half of these occasions companions joined them at the playback site within an hour. As well as emphasizing the value of having extra companions in an agonistic encounter, this result supports the hypothesis that roaring can serve to coordinate the activities of widely spaced group members (Schaller 1972).

That female lions carefully adjust their behaviour in contest situations according to the number of individuals in their own and the opposing group suggests that erroneous decisions to approach are costly and that individuals benefit by grouping whether they are defending a territory or passing through a territory owned by another pride (see also Packer 1986; Packer et al. 1990). The advantage that grouping confers in contests is likely to have provided an important selective pressure for sociality in lions and other group-living species that defend shared resources and, consequently, fitness benefits that could be derived from the development of numerical assessment skills.

These experiments provide the first empirical evidence that in contests between social groups opponents assess resource-holding potential on the basis of relative group size. Assessment of relative group size would be expected to take precedence over assessment of individual characteristics in other species where social groups compete for resources (e.g. Ligon & Ligon 1982; Whitehead 1987; Brown et al. 1988; East & Hofer 1991) and larger groups tend to dominate smaller ones in intergroup encounters (e.g. Harrington & Mech 1979; Sekulic 1982; Cheney 1986).

ACKNOWLEDGMENTS

discussion and comments on the manuscript. The research was supported by N.S.F. grant no. 8807702, the University of Minnesota and Newnham College, Cambridge.

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