

Maternal grouping as a defense against infanticide by males: evidence from field playback experiments on African lions

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Female lions roar in order to stay in contact with their pridemates and to defend their territory against other prides. In doing so, however, they risk attracting the attention of potentially infanticidal nonresident males. We used playback experiments to demonstrate that nonresident males are indeed specifically attracted to female roars, approaching the roars of female, but not male, conspecifics. However, there was also evidence that males adjust their behavior according to the probability that they might execute a successful takeover. Alien male lions were more reluctant to approach playbacks of three females roaring than of a single female roaring; single males were more reluctant than pairs to approach female roars; and old males were more reluctant than younger males to approach female roars. Previous observational studies have shown that female lions living in groups are more successful than singletons at defending their cubs in direct interactions with potentially infanticidal males. Our results suggest that maternal groups may also, by roaring in chorus, minimize the chances that these encounters occur at all. *Key words:* African lions, grouping, infanticide, playback experiments, roaring, vocal communication. [*Behav Ecol* 7:55–59 (1996)]

In lions (*Panthera leo*), as in a wide variety of other mammals (e.g., other carnivores: Packer and Pusey, 1984; primates: Leyland et al., 1984; rodents: Parmigiani et al., 1994), males that have newly entered a social group will kill or drive off all the dependent offspring of the resident females (Bertram, 1975; Packer and Pusey, 1983, 1984; Packer et al., 1988; Pusey and Packer, 1994). Male lions gain reproductive advantages from infanticide, since females whose maternal investment has been terminated exhibit estrus on average 8 months sooner than females whose cubs survive to independence (Packer and Pusey, 1984; Pusey and Packer, 1994). Female lions, however, suffer an immediate fitness loss and have evolved a number of strategies to reduce the risk of infanticide by males (Packer and Pusey, 1983, 1984; Pusey and Packer, 1994). These include retreating from the roars of unfamiliar males (McComb et al., 1993), avoiding new males that associate with other females in the pride (Packer and Pusey, 1984; Pusey and Packer, 1994), and grouping together to repulse intruders communally (Packer et al., 1990).

Pride females encounter extrapride males relatively frequently (on average once every 5 days in the Serengeti: Packer C, personal communication; from 141 days of 24 h observation of females) and mothers will risk injury and even death while defending cubs (Packer et al., 1990). Females with cubs will threaten and attack alien males, and groups of two or more females are much more successful at defending their cubs than are single females (Packer et al., 1990). Females with cubs of similar age tend to pool their cubs in a crèche and the mothers associate together as a group almost constantly (Packer et al., 1990). In contrast, nonmothers spend a considerable amount of time alone and associate with various other females in temporary “fission-fusion” sub-

groups (Packer, 1986; Schaller, 1972). Group defense of cubs against alien males has been cited as the best explanation for crèche formation and the tendency of females with cubs to remain in constant association (Pusey and Packer, 1994).

Both male and female lions roar to advertise territory ownership and to contact pride companions (Grinnell et al., 1995; McComb et al., 1994), and both sexes can efficiently discriminate the sex and number of unfamiliar lions from playbacks of their roaring (Grinnell, 1994; Grinnell et al., 1995; McComb et al., 1993, 1994). Because of the flexible nature of lion associations, lions may roar in mixed-sex choruses, in single-sex choruses, or alone. The tendency of females with cubs to associate with other mothers should make them more likely to participate in a roaring chorus than females without cubs. Playback experiments have already demonstrated that female lions are less likely to approach three females roaring in chorus than a single female roaring alone, and that approaches to choruses of three females are made more cautiously than approaches to single females (McComb et al., 1994). If the approach of extrapride males is similarly affected by the number of females roaring, group membership and communal vocal display by females with cubs may help to deter potentially infanticidal males.

Here we use playback experiments to investigate how roaring singly or in groups affects female vulnerability to infanticide. We test first, whether extrapride males are attracted to the roars of females and second, whether these males are more reluctant to approach choruses of three females roaring together than single females roaring alone.

METHODS

Study population

The lions involved in this study belong to adjacent populations in the Serengeti and Ngorongoro ecosystems in Tanzania. All individuals were recognizable from natural markings (Packer et al., 1988). Demographic records have been

maintained on lions in a 2000 km² area of the Serengeti National Park and in Ngorongoro Crater since 1974, and records on two prides in the Serengeti date back to 1966 (Bygott et al., 1979; Packer et al., 1988; Schaller, 1972).

Lion social organization and roaring

African lions live in stable matrilineal kin groups (prides) of 1 to 18 females, their dependent offspring, and a coalition of 1 to 9 males that enter the pride from elsewhere (Packer et al., 1988). Prides occupy exclusively defended ranges that are passed from mother to daughter, but individual pride members may be scattered in subgroups throughout the pride range (Packer et al., 1988). Nonresident males pass through pride ranges singly or in nomadic coalitions, and will kill cubs they encounter (Packer and Pusey, 1984; Schaller, 1972).

Lions are active primarily at night, and most roaring occurs at this time (Schaller, 1972); as roars are audible up to 5 to 8 km away, most roaring individuals are out of sight of other lions. When group members roar together the roars are delivered in chorus, with individuals overlapping each other's roars (Grinnell et al., 1995; McComb et al., 1994).

Playback experiments

We played to single nonresident male lions and nonresident males in coalitions of two (1) roars that had been recorded from either one, two, or three males that were unfamiliar to the subjects; or (2) roars that had been recorded from either one or three females that were unfamiliar to the subjects. We considered subjects to be unfamiliar with the roaring individuals if the playback was performed more than 30 km from the roarers usual range. All recordings used for playback were made using a Sennheiser MKH 816T directional microphone linked either to a Panasonic SV-250 digital audio tape recorder or a Sony Professional Walkman WM-D6C. We used five different recordings of males and eight different recordings of females in a total of 24 playbacks. All recordings of females roaring were from females known not to be in estrus at the time, and were of roars given spontaneously for apparent intrasexual territorial display. In previous playback studies, the male and female recordings used here were found to be free of bias (Grinnell et al., 1995; McComb et al., 1994).

Protocol

We conducted playbacks when the male subjects were not feeding and when there were no female lions in the vicinity. Where the same males were played, on separate occasions, recordings of one female and three females roaring (see below for details of these paired comparisons), we always separated these playbacks by at least 7 days to avoid habituating the subjects. We chose recordings according to the geographic location of the subjects (e.g., recordings of lions resident in the south would only be played to lions in the north) and how often each recording had been used in the study. We played a single bout of roaring 30 min before dusk using a Panasonic SV-250 tape recorder, a Proton or ADS P120 amplifier, and a Klipsch Heresy loudspeaker placed 200 m from the subject(s), and repeated it once after 5 min if the subject(s) had not moved. Peak sound pressure levels were 116 db at 1 m from the loudspeaker, and were equalized for each recording. We monitored the responses of subjects for 1 h from the onset of playback using a Sony CCD-F40 8 mm video camera and field notes.

Subjects responded to broadcast roars in one of three

Table 1

Responses of nonresident males to the roars of male and female lions

Sex of roarers	Approach	Don't approach
Male	0	6
Female	10	3

Fisher's exact test: $p = .0062$, two-tailed. The average number of roarers per playback was similar for both male and female playbacks: mean \pm SE; male: 2.0 ± 0.45 ; female: 2.1 ± 0.28 .

ways: (1) by approaching the loudspeaker; (2) by looking intently in the direction of the loudspeaker but not moving; or (3) by moving away from the loudspeaker.

When males approached the loudspeaker we recorded the latency (in seconds) from the onset of the broadcast roar until an approach began; the latency until the subject(s) came level with the loudspeaker; the number of times each subject paused during its approach and, when more than one subject was present, the number of times the leading subject looked back towards his companion. We noted non-approaches and moves away from the loudspeaker, but collected no additional information. We based the final analysis of approaches on measures of latency until level with the loudspeaker, which in this and previous studies provided the best single measure of the "cautiousness" of the approach (see Grinnell et al., 1995; McComb et al., 1994). When more than one subject was involved in the playback, we calculated a single mean value for coalition latency from individual approach times.

Hypothesis testing

Are extrapride males attracted to the roars of females?

To test this we compared the responses of coalitions of one or two extrapride males to playbacks of roaring from unfamiliar males and roaring from unfamiliar females. If males were subjects of more than one playback (5 of 13 coalitions played female roars), we included in our analysis only results from the less-represented playback size (that of three females). The average number of roarers was similar for both male and female playbacks (see Table 1). If males are differentially attracted to female roars they should be more likely to approach playbacks of unfamiliar females than those of unfamiliar males.

Are extrapride males more reluctant to approach choruses of three females roaring together than single females roaring alone?

To test this we compared the responses of extrapride males to recordings of single females roaring with responses to choruses of three females. To control for the identity of the individuals roaring in recordings of singletons versus choruses, playback sequences were chosen so that females roaring as part of choruses in the recordings of three females were also presented roaring alone in the recordings of single females (see also McComb, 1992). The order in which each male was presented one or three females was chosen arbitrarily.

Statistical analyses

Simple nonparametric tests were used in all comparisons. Because lions often failed to approach the speaker during playback experiments, thus making tests of absolute differ-

Table 2
Responses of single extrapride males to matched playbacks of one and three female roars

Lion	Age (years)	One female		Three females	
		Approach response	Latency to speaker(s)	Approach response	Latency to speaker(s)
GE-2	4.5	Running	166	Slow, cautious	2327
TRG	4.2	Fast walk	291	Very cautious	3666
PIMM	13.5	Slow walk	1048	No movement	—
U3H	11.5	No movement	—	Moves away	—
BOXER	8.2	No movement	—	No movement*	—

* See text for behavioral contrast.

ences in latency impossible, we categorized the data according to the age of the lion and the rate of his approach.

RESULTS

Male attraction to female roars

Nonresident males avoided the broadcast roars of unfamiliar males in all six cases, but often (10 of 13 coalitions) approached those of females. Six coalitions consisting of either one or two nonresident males never approached the roaring bouts from one, two, or three unfamiliar males. Indeed, three of the six remained in their original location, while the other three moved away from the speaker. In contrast, of 13 coalitions played roars from either one or three females, 10 approached the broadcast roars (Table 1: $p = .0062$, $n = 19$, Fisher's exact test, two-tailed). Simply by roaring, therefore, females may attract alien, and potentially infanticidal, males.

Effect of female group size on attraction of males

In five tightly controlled matched pairs comparisons in which single nonresident males were played the roars of one and three nonresident females on separate occasions, subject lions were less likely to approach the larger group in each case (Table 2: $p = .062$, sign test, two-tailed). Although one male (BOXER) remained stationary in response to both playbacks, he exhibited signs of intense agitation, such as is seen in nonresident males immediately prior to fleeing a strange male, only during playback of the trio roar (Table 2).

Two other factors appeared to influence the decision to approach female roars: the age and the group-size of nonresident males. Our results suggest that both may be important; however, age and group size were confounded by pairs always being composed of young males. We performed play-

backs of three females roaring to eight coalitions, five young (<7 years; two single males and three pairs) and three older, single males. The five coalitions of young males all approached the female trios, while none of the older males did so (Table 3: $p = .036$, $n = 8$ nonresident coalitions, Fisher's exact test, two-tailed). Additionally, the three pairs of young males all approached female trios in less than 500 s (mean = 345 s; range = 220–412 s), while single males both young and old never approached the roars of three females in less than 2300 s (Table 3: $p = .036$, $n = 8$, Fisher's exact test, two-tailed).

DISCUSSION

Extrapride males were attracted to roaring bouts from unfamiliar females, sometimes even running towards the loud-speaker in response to the playback. This was a function of the sex (rather than the unfamiliarity) of the roaring lions—playbacks of unfamiliar males roaring never elicited this response. In mammals, loud calls are often used to bring the sexes together for mating (e.g., elephants: Poole and Moss, 1989; humpback whales: Tyack, 1981; red deer: McComb, 1991; elephant seals: Cox and le Boeuf, 1977; other carnivores: Peters and Wozencraft, 1989). We have anecdotal evidence that estrous female lions, when lacking a consort, will roar to attract a mate: after we tranquilized the male of a consorting pair, the female moved away and began roaring during the middle of the day (when lions are usually inactive and silent: Schaller, 1972), stopping only when the male rejoined her after regaining consciousness. However, while both sexes would benefit from this attraction if the loud calls were used solely to indicate sexual receptivity, roaring by female lions has a predominantly intrasexual social function (McComb et al., 1994). Females roar to defend their territory and to establish contact with other pridemates (McComb et al., 1994; Schaller, 1972). However, females with cubs stand to incur substantial fitness losses if their roars attract potentially infanticidal males.

Females with cubs may be able to minimize the risk of attracting alien males by roaring as part of a female chorus. Male subjects were more reluctant to approach females roaring in a chorus of three than females roaring alone. There is evidence from long-term data on the study populations that females in groups of two or more are better able to successfully repulse alien males than are single females (Packer et al., 1990). Furthermore, as females with cubs are more likely to associate in groups (see introduction), groups will be more likely to contain the females that have the greatest incentive to attack alien males. The greater reluctance of extrapride males to approach female choruses is likely to reflect the increased risk of injury associated with approaching female groups as compared to single females.

Table 3
Rate of approach, age, and group size of extrapride males when presented with a group chorus of three females

Rate of approach	Young* pair	Young solitary	Older solitary
No approach	—	—	3
Slow approach (> 2300 s)	—	2	—
Fast approach (< 500 s)	3	—	—

* Less than 7 years.

Our experiments provide two further indications that males were adjusting their behavior according to the risk attached to approaching females. First, lone males appeared more reluctant to approach females roaring than did males with a coalition partner. Second, younger, more inexperienced males were less cautious in approaching female roars than were older males. While age and group size were somewhat confounded (see Results), our data indicate that both of these results may be important. The first undoubtedly reflects the "strength in numbers" phenomenon that also characterizes male approaches to unfamiliar males (Grinnell et al., 1995) and female approaches to unfamiliar females (McComb et al., 1994). A number of explanations are possible for the second result, but it is most likely that the assessed ratio of costs to benefits of approaching female roars varies with male age and experience. Older males are more likely to have experienced hostile receptions from female groups during previous encounters, and this may alter their assessment of the benefits of approaching. Also, if estrous females have qualitatively different roars from nonestrous females (note that all the recorded roars in this experiment were from nonestrous females), older males may be better able to discern the females' reproductive state and thus be better able to avoid groups of anestrus females. Finally, the costs of approaching may be higher for older males if their competitive abilities are reduced by age.

While extrapride males adjusted their approach to playback according to the number of individuals in their own group and the number of females they were approaching, the nature of the approach was significantly different from our previous playbacks of like-sex intruders to resident male and female lions (Grinnell et al., 1995; McComb et al., 1994). Resident lions approached alien male roars tensely, with their heads held low, whereas nonresident males approached female roars with their heads high as if looking for females. Furthermore, they frequently sniffed the ground or "flehmened" (grimacing to expose the vomeronasal scent organ) in the vicinity of the loudspeaker much as a male does around a potentially estrous female (Schaller, 1972). These searching approaches suggest an information gathering process lacking in the directed aggression of resident male approaches to the roars of male intruders, and imply that while looking for females, males may base their subsequent behavior on the behavior or group composition of the pride members they find (including the resident males).

Female lions that are nursing cubs roar for social reasons (see above). One by-product of this necessary social communication is the attraction of potentially infanticidal males. The greater reluctance of extrapride males to approach playbacks of three females roaring suggests that roaring as part of a chorus may be one way of minimizing the risks of infanticide. We would predict that females that are nursing cubs should always join in roaring choruses initiated by their pridemates. Moreover, roaring by single females with cubs should only be observed where other adult members of the pride can be recruited as a result of this vocal advertisement (i.e., truly solitary mothers—those with no pridemates—should not roar while they have cubs with them).

Roaring in a chorus may provide a means by which female lions with cubs can engage in essential territorial advertisement and social recruitment, while at the same time deter the approach of potentially infanticidal males. This could have parallels in other social species where infanticide represents an important selection pressure. In spotted hyaenas, *Crocuta crocuta*, where anecdotal evidence suggests that non-clan members will kill cubs at unattended dens, females with cubs give vocal displays at a higher rate than nonmothers and females call more often when intruder pressures are

high than when they are low (East and Hofer, 1991). East and Hofer (1991) suggested that both increases in call rate function to deter extrapride members from the den area.

Our experiments support the findings of previous observational studies, providing further evidence that membership in a social group decreases the risk of infanticide (see Packer, 1986; Packer et al., 1990; Pusey and Packer, 1994). They suggest that female lions with cubs may benefit by associating in a group not only because this makes them more successful than single females at defending their cubs during direct encounters with extrapride males (Packer et al., 1990; Pusey and Packer, 1994), but also because by advertising their group size in bouts of communal roaring they minimize the risk that these encounters will occur at all.

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