



Roaring and social communication in African lions: the limitations imposed by listeners

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In some social mammals, loud calling not only serves to advertise ownership of a territory and attract mates but also plays a vital role in allowing social companions to maintain contact when they are separated by long distances. Under these circumstances, individuals that are not territory owners but that call in the context of social cohesion or mate attraction could risk inviting escalated contests from territorial competitors. Here we present observations and playback experiments demonstrating that nomadic male lions (*Panthera leo*) do not roar despite the likely importance of roaring in maintaining social ties with other males in their coalition, on which their subsequent reproductive success depends. Instead, roaring is confined to males that are resident in prides and prepared to escalate in contest situations. Roaring is a flexible behaviour that is sensitive to temporal changes in status; resident males remain silent outside of their territories even when presented with playbacks of unfamiliar males roaring, and nomadic males start roaring only when they are taking over a pride. Our study suggests that individuals of social species may avoid giving important long-distance signals in circumstances where it would pay them to conceal their presence from eavesdroppers.

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Loud, long-distance vocal signals often serve a number of different functions simultaneously. Song in male birds, for example, not only functions in territorial defence, but is also used to attract mates and can advance female ovulation (Catchpole & Slater 1995). Similarly, some male mammals have loud calls that serve multiple functions within the context of reproduction and indeed these functions can be entirely compatible if the signaller is both ready to engage in male–male competition and to mate with females (e.g. red deer: Clutton-Brock & Albon 1979; McComb 1987, 1991). However, there are situations in which signals that would be beneficial in one of these multiple contexts may be costly in another; for example, where an individual male could gain reproductive advantages by signalling to attract mates but in doing so would invite escalated contests with male competitors.

The potential for such conflict is likely to be considerable in social mammals that use loud calls not only in territorial defence and mate attraction but also to maintain contact with widely spaced social companions (e.g. wolves: Harrington & Mech 1979; lions: Grinnell &

McComb 1996; McComb et al. 1994; chimpanzees: Mitani & Nishida 1993). Here we might predict that particular classes of individuals that cannot afford to incur the costs of escalated encounters with listening competitors might remain silent even though, by doing so, they could stand to forfeit the benefits of coordinating their movements with members of their own social group.

African lions, *Panthera leo*, are one of the social mammals in which this conflict of interest is relevant. The stable units of lion social organization are prides, consisting of matrilineal kin groups of 1–18 females, their dependent offspring and a coalition of 1–9 resident males that enter the pride from elsewhere (Packer et al. 1988). In the pride, both sexes roar in order to broadcast ownership of a territory, to stay in contact with other members of their social group and, under some circumstances, to attract mates (Schaller 1972; McComb et al. 1994; Grinnell et al. 1995; Grinnell & McComb 1996; Funston 1999). At any one time, however, a high proportion of male lions in the population are not in possession of a pride (10-year mean for 1981–1990: 1.37 nomadic males per resident male, unpublished data). These individuals wander widely, passing through pride ranges singly or in coalitions until they are successful in taking over a pride of their own (Hanby & Bygott 1987; Pusey & Packer

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1987). It is paramount for these nomadic males to gain and maintain social bonds with their companions while they wander because success in competition for prides is strongly dependent on group size (Bygott et al. 1979; Grinnell et al. 1995). Roaring provides a means by which nomadic males might co-ordinate their movements with coalition partners or recruit new ones (see also: McComb et al. 1994; Grinnell et al. 1995). However, if nomads used this loud long-distance signal to communicate with social companions they would also advertise their position to resident males in the area.

The costs to nomadic males of engaging the attention of resident males may be considerable. Resident male lions consistently give aggressive approaches to playbacks of roaring from strange males broadcast in their territories (Grinnell et al. 1995) and observations indicate that real intercoalition encounters may be fatal (Schaller 1972; Grinnell et al. 1995). Under these circumstances, nomads might benefit by reducing their rate of roaring or even abandoning roaring altogether and concealing their presence, despite the detrimental effects that this might have on their ability to maintain contact with coalition partners and potentially attract mates. We used a combination of observation and playback experiments to examine: (1) whether nomadic males show lower rates of roaring than resident males; (2) whether roaring behaviour provides a reliable indication of willingness to escalate in a contest with other males; and (3) whether roaring behaviour is sensitive to temporal changes in residence status.

METHODS

Study Population

The lions in this study consisted of 20 resident and 11 nonresident male coalitions in two adjacent populations in the Serengeti and Ngorongoro ecosystems in Tanzania (see Packer et al. 1988 for further details). All the lions were individually identifiable from natural markings and territory boundaries for resident coalitions had been established from daily sightings data. Continuous demographic records have been maintained on lions in a 2000-km² study area in Serengeti National Park and in the entire Ngorongoro Crater since 1975; records on two of the Serengeti prides date back to 1966 (Schaller 1972; Packer et al. 1988).

Lion Roaring

Roars are loud, low-pitched vocalizations that are delivered in bouts, which typically last 30–60 s and consist of several soft introductory moans, a series of full-throated roars and a terminating sequence of grunts (McComb et al. 1994; Grinnell et al. 1995). The roaring sequences used in our playback experiments (see below) all consisted of full bouts recorded from adult males. Lions are active primarily at night, and most roaring occurs during nocturnal hours (Schaller 1972; Hanby et al. 1995).

Observations of Roaring Behaviour

We visually followed radiocollared male lions by vehicle on moonlit nights using light-intensifying

goggles, while taking care to minimize possible interference with the lions' behaviour. We recorded the contexts and behaviours associated with bouts of roaring in field notes, and, when possible, the roar itself on audio tape (see below). These observations were concentrated in the period from December to May, when both resident and nonresident coalitions are visible in the study area.

Sound Recording and Playback Experiments

We made recordings of lion roar sequences using a Sennheiser MKH 816T directional microphone linked to a Panasonic SV-250 digital audio or a Sony WM-D6C cassette-tape recorder. We made all recordings used for playbacks in conditions of low air turbulence and at distances of less than 30 m from the vocalizers. The vocalizers in these recordings consisted of single males or groups of two or three males roaring in chorus.

We conducted playback experiments on male subjects only when they were not feeding and when no females were present. For each playback experiment we played recordings of individuals whose normal range was more than 30 km away, and thus could be considered unfamiliar to the subjects being tested. A single bout of roaring was played 20 min before dusk from a Panasonic SV-250 digital audio tape recorder, a Proton amplifier and a Klipsch Heresy loudspeaker, placed at 200 m from the subjects and concealed in available vegetation. Playbacks were repeated once after 5 min if the subject(s) did not move. Peak sound pressure levels for all playback experiments were 116 dB at 1 m from the loudspeaker. We recorded the responses of subjects for 1 h from the onset of playback using a Sony CCD-F40 8 mm camcorder and field notes. To avoid habituation, we always separated individual playbacks to the same subjects by at least 7 days.

Previous experiments have indicated that the responses of male lions to playback are usually clear-cut (Grinnell et al. 1995; Grinnell & McComb 1996). We scored the responses of playback subjects according to (1) whether they approached the loudspeaker and (2) the time between the start of playback and the arrival of approaching subjects at the level of the loudspeaker. We also monitored the number of times they paused and the number of times they looked around at companions during the approach but these data were not used in the analyses presented here. We also monitored the number of roaring bouts given by subjects in the hour following playback.

Hypothesis Testing

Who roars?

To ascertain whether nomadic males roared at lower rates than resident males, we conducted nocturnal 6-h focal animal observations on 12 resident coalitions ($N=21$ nights) and six nonresident coalitions ($N=10$ nights). In addition, we conducted 48-h continuous observations on three of the resident and one of the nonresident coalitions (bringing the total nights observed to 27 for residents and 12 for nonresidents).

Table 1. Comparison of roaring rates of resident and nonresident male lions during nocturnal observations from 1800 to 2400 hours

Resident coalition	Coalition size	Roar bouts per lion per h	Number of hours	Nonresident coalition	Coalition size	Roar bouts per lion per h	Number of hours
1. BOMAS	3	1.94	6	1. GI	2	0.0	18
2. HMO	2	0.50	9.5	2. Achilles	2	0.0	12
3. Magadi	2	0.33	6	3. L21	1	0.0	3
4. JMS	3	0.75	12	4. SN27, 29	2	0.0	6
5. MSMS	4	1.13	19	5. Timoteo	2	0.0	12
6. SNORM	2	0.75	18	6. JM	2	0.0	11
7. LTWIRP	3	0.75	10				
8. MMS	2	0.33	18				
9. PIM#5	2	1.67	12				
10. GJO	2	1.67	12				
11. LXX,S	2	0.08	6				
12. SNCH	2	2.00	5				

Mann-Whitney U test: $U=66$, $N_1=12$, $N_2=6$, $P<0.001$.

Is roaring a reliable indication of willingness to escalate?

To determine whether willingness to escalate is confined to categories of males that roar, we conducted playback experiments on a sample of resident males (that did roar during our observational study; see Results) and of nomadic males (that did not roar during our observational study; see Results). The ratio of the number of subjects to the number of individuals roaring from the loudspeaker was kept at approximately one to control for any variation in responses due to this factor (McComb et al. 1994; Grinnell et al. 1995; Grinnell & McComb 1996). Prior work has demonstrated that the responses of one, two or three subject lions are indistinguishable from each other when challenged by playbacks matched to the defenders' group size (Grinnell et al. 1995). Eleven coalitions containing one to four resident male lions (mean \pm SE: 2.27 ± 0.27) were thus played comparable numbers of unfamiliar males roaring (1, 2 or 3: 2.09 ± 0.25) while well inside their pride territory. We compared their responses to those of six nonresident male coalitions comprised of one to three (1.50 ± 0.34) individuals that were played recordings of one to three (1.67 ± 0.33) males roaring. We used a total of 11 recordings of 11 different coalitions in these experiments. When a coalition was subject to more than one playback experiment, we included only one response per coalition by choosing the experiment in which the number of intruders played was most similar to the number of defenders present. When several experiments yielded equivalent 'odds', we chose that experiment in which the greatest fraction of the defending coalition was present. However, in our experiments, coalitions were consistent in their behaviour across playbacks, with each coalition responding similarly to all playbacks in a given context.

Is roaring behaviour sensitive to temporal changes in residence status?

To determine whether roaring behaviour changes with residence status we performed two comparisons.

(1) We compared the responses of 11 coalitions of resident males to playbacks of roaring from unfamiliar males while they were well within their pride territories to those of five different resident coalitions of males that were outside their territorial boundaries; as before, we chose playback sequences to match the number of roarers with the number of subjects (mean \pm SE inside: 2.27 ± 0.27 subjects versus 2.09 ± 0.25 roarers; outside: 2.20 ± 0.20 subjects versus 2.40 ± 0.25 roarers). We used a total of 13 recordings of 12 coalitions in these experiments.

(2) We had the opportunity to observe four coalitions both as nonresidents and later when they became resident in prides (see Results). We observed these coalitions for a total of 95.5 h as nonresidents, and 90.5 h as residents.

Statistical Analyses

We used nonparametric statistical tests throughout due to small sample sizes and non-normal data distributions. We rejected the null hypothesis when significance tests produced a two-tailed probability of less than 0.05.

RESULTS

Who Roars?

The 12 coalitions of resident males gave an average \pm SE of 0.99 ± 0.19 roar bouts per lion per h over the period of observation. In contrast, none of the six coalitions of nonresident males observed ever roared (Table 1; Mann-Whitney U test: $U=66$, $N_1=12$, $N_2=6$, $P<0.005$). Roaring was thus confined to resident males.

Are Roarers Willing to Escalate?

All 11 resident coalitions approached the loudspeaker when they were challenged with unfamiliar males and nine of the 11 roared in the hour following the playback

Table 2. Behaviour of resident and nonresident coalitions when challenged by playback of unfamiliar males roaring

Coalition type	Approach the speaker*		Roar in hour following playback†	
	Yes	No	Yes	No
Resident	11	0	9	2
Nonresident	0	6	0	6

*Fisher's exact test: $P < 0.0001$.†Fisher's exact test: $P < 0.005$.**Table 3.** Behaviour of resident male coalitions when challenged by playback of unfamiliar males roaring inside and outside of their pride territory

Location	Approach the speaker*		Roar in hour following playback†	
	Yes	No	Yes	No
Inside	11	0	9	2
Outside	0	5	0	5

*Fisher's exact test: $P < 0.0005$.†Fisher's exact test: $P < 0.005$.

experiment. In contrast, none of the six nonresident coalitions played unfamiliar males roaring approached the loudspeaker (Table 2; Fisher's exact test: $N=17$, $P < 0.0001$) or roared in the hour following playback (Table 2; Fisher's exact test: $N=17$, $P < 0.005$). Instead, three coalitions silently moved away from the speaker and three made no move. Thus escalation was confined to the category of males that roared (resident males).

Is Roaring Behaviour Sensitive to Temporal Changes in Residence Status?

(1) As reported above, 11 resident coalitions challenged with playbacks while well inside their territories responded by aggressively approaching the speaker. In comparison, the five resident coalitions played strange males roaring while well outside their territory boundaries did not approach the speaker (Table 3; Fisher's exact test: $N=16$, $P < 0.0005$). Furthermore, only resident males that were actually on their territories responded to

playback by roaring in the hour following it (Table 3; Fisher's exact test: $N=16$, $P < 0.005$). Thus, roaring and escalation by resident males were confined to situations in which the males were actually on the territory where they were resident.

(2) The four coalitions observed as silent nonresidents were all later observed roaring when they became resident with a pride. Thus roaring behaviour changed with changing residence status (Table 4).

DISCUSSION

In our study, only male lions that were resident in a pride were ever observed roaring. We never observed nomadic males roaring when we followed them, even when they were separated from their coalition partners. They also failed to roar when presented with playbacks of unfamiliar males roaring. In contrast, resident males maintained a high rate of roaring during follows and usually roared in the hour following playbacks of roaring from unfamiliar males. Thus nomadic males in our study area do appear to refrain from roaring.

This restraint could reflect two situations: (1) nonresident males gain no benefits from roaring and thus never do so, or (2) nonresident males would gain from roaring, particularly by enhancing their ability to recruit and maintain contact with coalition partners (see also McComb et al. 1994; Grinnell et al. 1995), but the costs associated with it outweigh the benefits. The first suggests that nomadic males should never roar under any circumstances, whereas the second predicts that nomadic males will only roar when the probability of incurring costs, specifically the risk of attracting the attention of resident males in the area, is low. Two sets of observations suggest that the latter interpretation is correct. First, observations by Funston (1999) on nomadic male lions in Kruger National Park, South Africa, indicate that there nomadic males do occasionally roar, but at greatly reduced rates compared with resident males. Of the three nomadic coalitions that he observed (each for 21 nights or more), males in one coalition ('J Males') were explicitly noted to spend most of their time in an area without resident males and thus where the social costs to roaring would be reduced. Second, recent observations of our own in Pilanesberg National Park, South Africa, suggest that there nomadic males also roar when local resident males are unlikely to hear them. Pilanesberg, an ancient volcanic caldera, contains valleys that are acoustically isolated

Table 4. Male coalitions observed both while nonresident and later while resident with a pride

Coalition	Nonresident		Resident	
	Number of hours observed	Roar bouts per lion per h	Number of hours observed	Roar bouts per lion per h
JMS	11	0.0	21.5	0.37
GI	33.5	0.0	48	0.85
LTWIRP	3	0.0	17	0.28
TIMO	48	0.0	4	4.00

from other such valleys by mountainous ridges. We observed a nonresident male coalition roaring in one of these valleys that was not occupied by resident males or females. In contrast, in our Serengeti and Ngorongoro study areas, which are relatively flat and open, nomadic males were never observed to roar. Roars in such environments are likely to be heard by resident males from great distances.

Low signalling rates have been reported in other species in situations where conspicuous signals could attract the attention of potential competitors. Chimpanzees, *Pan troglodytes*, have been observed to remain unusually silent during excursions into the territories of other communities (Goodall 1986). Lone grey wolves, *Canis lupus*, howl less (if at all: Harrington & Mech 1979) and defecate and urinate less along trails (Rothman & Mech 1979) than territorial pairs and packs. Transient coyotes, *Canis latrans*, likewise howl at greatly reduced rates compared with residents when passing through others' territories (Gese & Ruff 1998). Cases of signals being difficult to locate in reproductive contexts where signallers would benefit by avoiding the attentions of competitors have also been observed (McGregor & Dabelsteen 1996). Indeed, nonresident male lions will approach pride females roaring alone, for example, but always do so silently (Grinnell & McComb 1996). Nonresident males may thereby gain matings without confronting the local resident males. It is interesting that resident male lions may also adopt an apparently stealthy strategy when ranging outside of their territory. In anecdotal observations (19 h of nocturnal follows) we noted that resident males that had ventured well beyond their territory boundaries never roared even when separated from coalition partners.

Our results show clearly that in the Serengeti and Ngorongoro crater, male lions only roar when they are prepared to escalate and that roaring whilst in the territory of resident males will invite an attack. Resident males both roared and approached the loudspeaker aggressively when played unfamiliar males roaring. The category of males in our study that never roared (nomadic males) also failed to approach playbacks. In the one context in which resident males did not roar (i.e. when they were presented with playbacks of unfamiliar roaring while outside their territory boundaries) they also failed to escalate against the roarers. It is also the case that while nomadic males in this study did not roar, we watched males that had been nomadic begin roaring as soon as they launched a challenge for ownership of a pride. This emphasizes that roaring is a flexible behaviour that signallers may adjust according to the consequences of revealing locational information to listeners.

McGregor and others have argued that communication is more appropriately viewed as involving a network of signallers and receivers rather than discrete signaller-receiver dyads, as any receivers within range of the signaller may extract information from the signalling event (McGregor & Dabelsteen 1996; Oliveira et al. 1998). This is particularly relevant to acoustic signals used for long-distance communication, where the area over which the signal is broadcast is often sizeable and typically

includes many potential listeners (McGregor & Dabelsteen 1996; Otter et al. 1999; McComb et al. 2000). Some of these listeners will inevitably be unwanted, effectively eavesdropping on a signal that is intended for other receivers. Our results indicate that nomadic males avoid roaring until they have gained prides and resident males temporarily refrain from roaring while they are outside of their own territories, despite the constraints that this is likely to place on their abilities to maintain contact with social companions. Long-distance acoustic signalling is likely to be controlled in similar ways in other social species in which eavesdroppers can impose high costs on signalling.

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