Chapter 3. Roaring and territoriality in male lions

Loud calling in mammals can function in intermale competition when rival males engage in vocal endurance contests. Red deer stags attempt to match the roaring rate of a rival and when unable, retreat without escalating (Clutton-Brock & Albon 1979). Red howler monkeys (Sekulic 1982) and elephant seals (Shipley et al. 1981) may similarly engage in intermale vocal battles, but this has yet to be rigorously demonstrated. Male loud calls may function as a form of male-male competition even in the absence of an immediate rival if the call conveys information about the resource holding potential (RHP) or aggressive intent of the male. Such vocal assessment may be an important aspect of intermale and intergroup competition in species that give loud calls audible to conspecific rivals, such as wolves (Harrington & Mech 1983, Harrington 1987), African elephants (Poole et al. 1988), lions (Schaller 1972; McComb et al. 1994; Chapter 1), and perhaps certain cetaceans (humpback whales: Tyack 1981; dolphins: Connor et al 1992), among others. For efficient discrimination of resource holding potential in loud calls, cues to the size, sex, motivation and location of a rival must be available to the listener. When competition is between social groups rather than individuals, however, the number of callers will often be of greater importance than their size (McComb 1992). In social situations such as these wherein loud calls can originate from either an ally or a rival, differentiating between the calls of group-member and competitor should be promoted by natural selection for immediate fitness reasons (e.g.. McComb et al. 1993).

Vocal cues that are useful for assessment of these traits are likely to be of five types: structure, pitch, intensity, rate, and complexity. Although song complexity has been shown to be important in male-male assessment in birds (e.g.. Krebs et al. 1978; Yasukawa & Searcy 1985; Baker 1988), lions show no similar variation in call type or repertoire, but rather share a stereotyped loud call of one basic structure. A typical lion roar sequence can be divided into elements of three distinct types: low intensity "preludes" that sound much like contact calls, followed by high intensity "roars" characterized by rising and then falling frequencies, and often ending with a series of staccato and atonal "grunts" (Fig. 1). Apart from this basic structure, the distribution of energy across harmonics and other more subtle vocal traits could provide cues to an individual's size or motivation as demonstrated by McComb (1988) in red deer stags.

While the basic pitch of a loud call--its fundamental frequency--has been shown to be negatively correlated with body size in anurans (Davies & Halliday 1978; Ryan

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1980) it has been demonstrated in few other groups. The fundamental frequency of a loud call is a function of the size and mass of the vocal cords as well as the rate of air flow through them. In mammals, air flow will depend on the effort of the chest and thoracic muscles during the call, such that greater effort will result in a higher pitch. There is no good a priori reason, therefore, to assume that pitch will correlate with body size in species such as lions; variation in effort is likely to confound any correlation between the size of the vocal cords, body size and pitch (McComb 1988). While this assumption deserves to be examined in greater detail, the relationship between pitch and RHP lies outside the scope of this thesis.

The intensity of a call, as an accurate indicator of effort, condition and RHP in species which engage in vocal contests (e.g.. red deer, Clutton-Brock & Albon 1979) and those which broadcast their calls to distant rivals (e.g.. wolves, lions, elephants), is likely to be of great importance in male-male assessment. However, absolute intensity is difficult to assess from recordings for a number of reasons. The intensity of a vocalization decreases inversely with the square of the distance from its source, and is attenuated by factors such as reflection of sound from the lion's body and the ground, absorption by the ground and by vegetation, and absorption by the air (Wiley & Richards 1978). Wind speed and direction, air temperature and relative humidity, and the orientation of the lion in relation to the microphone will all affect the sound intensity recorded at the microphone and make an assessment of absolute sound pressure very difficult. The role of absolute intensity in vocal assessment will therefore not be addressed here. Rather, a relative measure will be employed. The harmonic structure of a vocalization changes with the rate of air expulsion through the vocal cords, with relatively greater amounts of energy found in the higher frequencies of higher-intensity calls (Frokjaer-Jensen & Prytz 1976). This change in structure with effort is audible in lion roar sequences, and allows assessment of the relative intensity of a roar in relation to others.

The rate of roaring--the number or roar sequences per unit time--can easily be measured. Like intensity, how often an individual roars can be a measure of either condition or motivation, or a mixture of both. Roaring is likely to be energetically costly (Ryan 1988), and when engaged in roaring contests with rivals, high roaring rates can be an honest indicator of overall muscular condition, and thus of fighting ability (Clutton-Brock & Albon 1979; McComb 1988). In lions, most roaring occurs in the absence of obvious rivals and thus roaring rates in male lions will rarely give an accurate indication of maximum sustainable effort and therefore condition (cf. red deer: Clutton-Brock & Albon 1979). Instead, the rate of roaring by males could function as a conventional signal
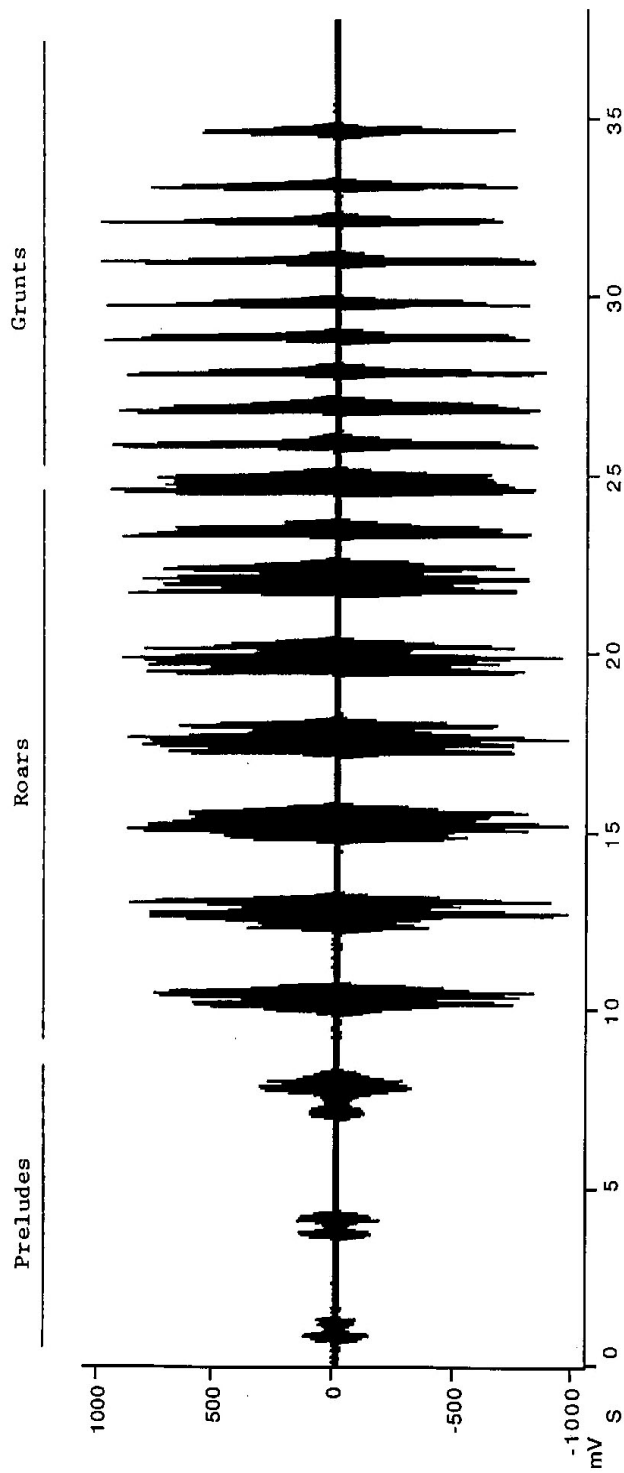
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Figure 1. Sound pressure level waveform view of a typical lion roar. Note that this roar contains 3 preludes, 8 roars, and 9 grunts.

announcing aggressive intent. Conventional signals not directly associated with RHP can be used to resolve contests if individuals signaling high aggression pay a cost when meeting each other (Maynard Smith & Harper 1988; e.g.. the state of musth in male African elephants, Poole 1989); in lions, encounters between male coalitions often result in serious wounding or even death (Chapter 1). While the roars of male lions are likely to convey some information on RHP, (such as the coalition size in a group chorus), and condition (see Discussion), information on the motivation of roaring males may likewise serve to deter rivals.

In this chapter I examine the function of roaring in advertising ownership status and territorial intent, and its role in discrimination of stranger from ally, male from female, and territoriality.

GENERAL METHODS

Playback Experiments

I performed playback experiments using roar sequences of known lions recorded on a Panasonic SV 250 portable digital audio tape recorder through a Sennheiser MKH816T directional microphone. I played back from digital tape the recording of a single bout of roaring of 1 to 3 lions lasting 25 to 55 seconds through a Proton 100 watt/channel amplifier and a single Klipsch Heresy speaker placed 200m from the subject lions. Playbacks commenced approximately twenty minutes before dusk (typically 1830 hours) and peak sound pressure levels were 116 dB at 1m. Tape and amplifier were controlled from within the vehicle while the speaker was concealed in vegetation 80-100m away. If no suitable cover was available, I placed the speaker adjacent to one end of the vehicle. If the lion(s) had not moved after five minutes, the roar sequence was repeated, and the subjects were monitored for at least an hour from the onset of the playback. I recorded all roar sequences given by the subject lions in that time whenever possible. Successive experiments to any one subject were separated by at least 7 days.

For every experiment, I videotaped the response of the lead lion(s) using a Sony CCD-F40 8mm videocamera equipped with a JVC directional microphone. Lions would typically respond either by approaching the speaker, remaining in place while looking in the direction of the speaker, or by moving away.

Naturalistic Observations

Serengeti lions are primarily active at night (Schaller 1972) and roar most frequently during nocturnal hours (Schaller 1972; Hanby, Bygott & Packer in press). I conducted nocturnal six-hour (1900-0100 hrs) focal-animal observations on 10 resident coalitions (n=21 nights) and 9 non-resident coalitions (N = 11 nights), and recorded roars on digital tape. In addition, 48-hour continuous observations were conducted on 4 resident and one non-resident coalition with the assistance of Dr. Karen McComb. I visually followed radio-collared lions by vehicle on moonlit nights using light-intensifying goggles, while taking care to minimize possible interference with the lion's behavior. Behavioral and weather observations were recorded every 15 minutes.

Analysis Of Recorded Roars

I scaled the relative intensity of a roar sequence from 1(high) to 3 (low) and quantified the number of preludes, roars and grunts for each male roar sequence while listening to the recording. Representative roar sequences were viewed with the computer software package Canary (Charif et al. 1993).

METHODS AND RESULTS

Roaring as a territorial display

In 13 nights (98 hours) that 7 different nomadic coalitions were followed, non-resident lions were never observed to roar. In contrast, in 20 out of the 24 nights (191 hours) that resident lions were followed (12 different coalitions), resident males always roared at least once each night (P = 0.0002, X^2=13.7 by night; P = 0.008, X^2=7.0 by coalition). Observations of nomadic males that become resident for short periods with solitary females also indicate that male lions only roar when they have been in recent association with females or are otherwise "resident" in a pride. Two solitary females on the plains attracted four different coalitions of males during two wet seasons and in each case the males were observed to roar while thus "temporarily" resident. In addition, four coalitions followed both while resident and while non-resident were only observed to roar during the resident follow. Roaring thus appears to be limited to males that are resident with females.

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If roaring is associated exclusively with territorial males, one might expect resident males to refrain from roaring when found well outside of their territory. I tested this with playbacks of unfamiliar single-male roar sequences to males from 16 resident coalitions. Roar sequences were broadcast to 5 coalitions when well outside their territory, and all behaved as non-residents: they looked intently towards the speaker but did not approach and did not roar in the hour following playback. All 11 of the other coalitions that were played unfamiliar roar sequences while within their territory approached aggressively and roared at least once in the following hour (Fisher's Exact Test, $P = 0.0002$, one-tailed). Roaring is thus associated both with resident status and with presence on the defended territory.

Advertising group membership

Coalition males often roar together, with one male initiating the roar sequence and each subsequent male joining in as the roar progresses. Group choruses thus typically consist of two or more partially overlapping roar sequences. Listeners could interpret overlapping roar sequences either as a coalition roaring together or as individual competitors responding to each others' roar sequences. Resident males would benefit from advertising their maximum coalition size to deter the intrusion of smaller rival groups. One method to achieve this result would be to modify the roar sequences in such a way as to make it apparent that all males are roaring together. Duets in various species may serve such a function (e.g.. gibbons, Raemaekers et al. 1984; review of avian species, Farabaugh 1982). Roaring lions may also "duet" by modifying the number of each roar element and their timing when roaring together.

I calculated the fraction of roar sequences initiated by each of 11 males for which group recordings exist in which that male terminated its roar sequence with more grunts than those males joining the roar. In 9 out of the 11 males initiating roar sequences with companions, the initiator grunted more than his companions in more than 50% of the roars (Table 1; $P = 0.03$, binomial). The two exceptions were companions of males who consistently included more grunts regardless of whether they initiated the roar sequence. While this individual variation is not surprising, it is notable that in most cases the role ("initiator" or "responder") took precedence over individual differences. In addition, all of the roar sequences of the 11 males recorded initiating roars possessed grunts, while 5 out of the 12 males that joined roar sequences included no grunts in at least one roar

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Table 1. Percentage of recordings for which each male had more grunt (G) and roar (R) elements than companions roaring simultaneously

	Initiators:				Responders:		
	Number of Recordings	% More G	R		Number of Recordings	% More G	R
JOE	6	0	100	GI	5	100	0
L21	1	100	100	L21	3	37	66
MM1	2	100	0	MM1	1	0	50
MM2	2	100	100	MM2	2	0	100
NORM	12	58	75	NORM	13	0	69
PLBLK	5	40	80	PLBLK	6	0	100
PLBLND	6	100	0	PLBLND	5	60	20
SBI	3	100	100	SBN	3	0	0
SNAG	12	100	33	SNAG	11	36	27
TWIRP1	5	80	40	TWIRP1	8	12.5	12.5
TWIRP2	8	71	71	TWIRP2	3	0	100

sequence (P < 0.05, X^2 = 3.9). Group-roaring males may also space roar and grunt elements such that they land in the pauses of their were companions of males who consistently included more grunts regardless of whether they initiated the roar sequence. While this individual variation is not surprising, it is notable that in most cases the role ("initiator" or "responder") took precedence over individual differences. In addition, all of the roar sequences of the 11 males recorded initiating roars possessed grunts, while 5 out of the 12 males that joined roar sequences included no grunts in at least one roar sequence (P < 0.05, X^2 = 3.9). Group-roaring males may also space roar and grunt elements such that they land in the pauses of their companion's roar sequence (e.g. Fig. 2), and may be more likely to intersperse roar and grunt elements (e.g. Fig. 3). While many functional explanations could account for these behaviors, one consequence will be the honest advertisement of group size: individual lions are incapable of producing a group chorus, and both male and female lions are able to assess the number of individuals roaring together (Chapter 1; McComb et al. 1994).

Announcing aggressive intent

While group choruses will serve to advertise the size of a coalition, resident males also appear to increase the rate and structure of their roar sequences in response to a perceived threat. After coalitions of 1-3 resident male lions were presented with the broadcast choruses of 1-3 unfamiliar males roaring together, I noted the number of roaring bouts initiated by the resident coalition in the following hour (typically from 1830 to 1930). In those cases in which a coalition was a playback subject on more than one occasion, the roaring rates were averaged into a single score per coalition. These roaring rates were contrasted with non-playback results from naturalistic observations of resident males (see "Roaring as a territorial display" above) begun by 1830 hours; the average rate of roaring was calculated for the period between 1800 and 2000 hours to approximate the same time of day measured for post-playback roaring. When a coalition was followed more than once, roaring rates were averaged. Note that wind speed affects the rate at which lions roar: males tend to roar less in higher winds (R^2 = .086, F=4.3, p<.05). However, no substantial differences existed in windspeed after playbacks and during naturalistic observations (mean ± SE: pb (n=14 coalitions), 2.71 ± 0.67 mph; observations (n=11), 3.96 ± 0.68; z=1.37, NS, Mann-Whitney).

Resident male lions roared significantly more frequently in the hour immediately following the playback of one or more intruder males than at similar times when not presented with simulated intruders (Fig. 4: P < 0.02, z = 2.41, Mann-Whitney).
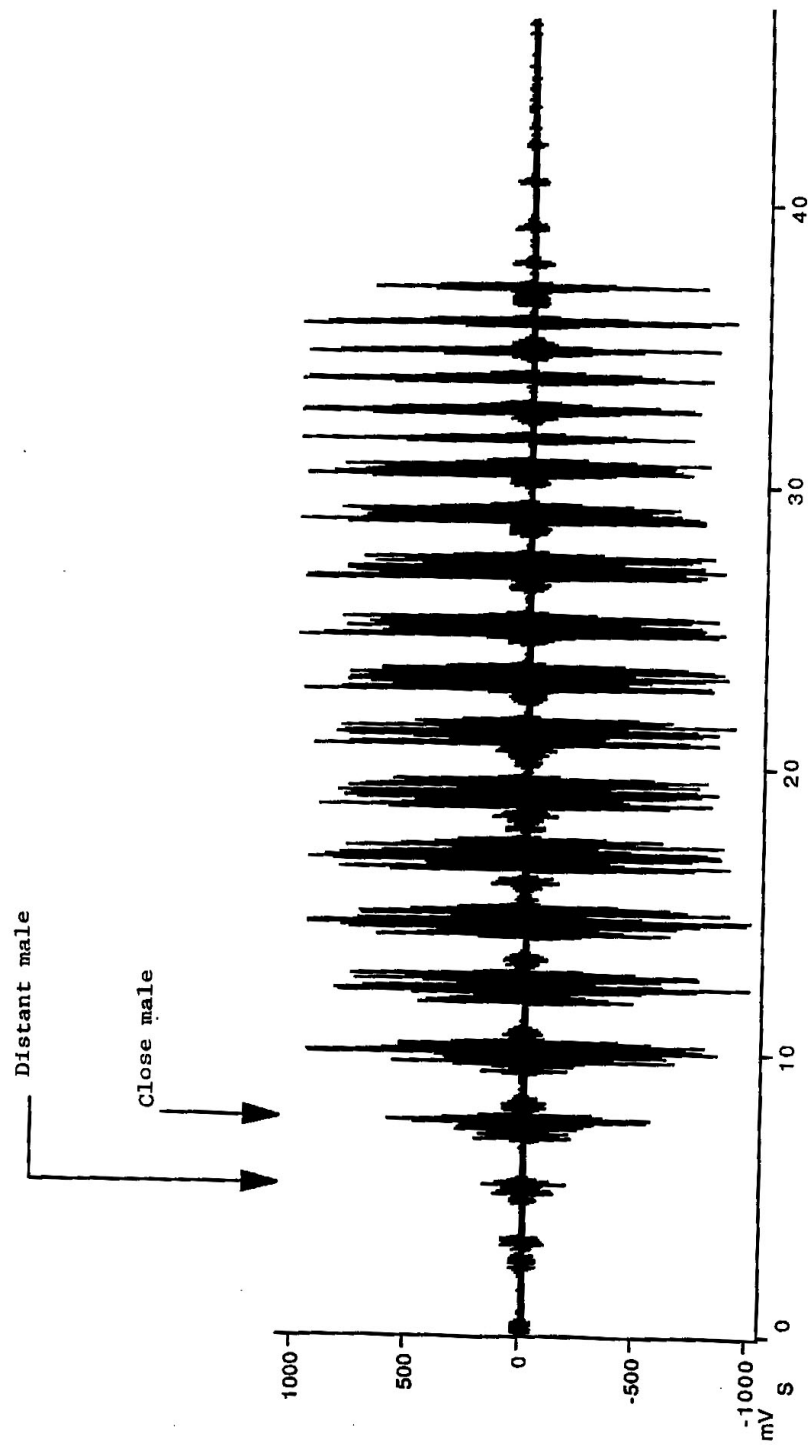
Figure 2. Spacing of roar elements when two males roar together. The waveform trace of the distant male that initiated the roar sequence is smaller than that of the closer male that joined.
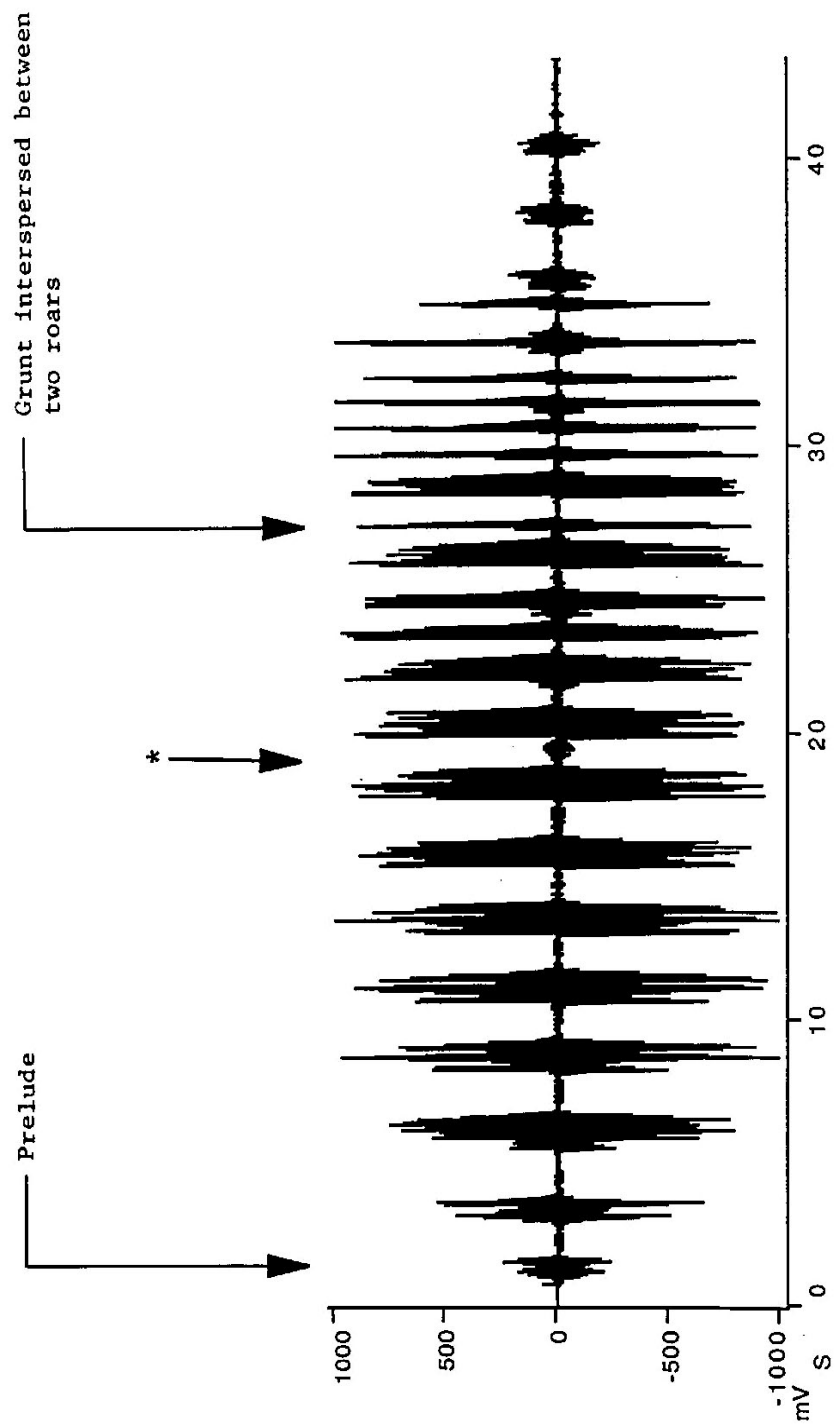
Figure 3. Interspersion of roar and grunt elements when roaring with another coalition male. Note the grunt between the 12th and 13th roars (one prelude precedes the roars). * marks the point at which a responding male joined the initiated roar sequence.

However, the vocal response of resident males to intruders was not proportional to the perceived threat: the number of males present for the playback experiment, the number of intruders simulated, the ratio of intruders to defenders, and the absolute coalition size of the defending coalition all were uncorrelated to the number of roars given ($R < .15$, $P > 0.4$ for all). Rather, an intruder threat appears to be met by an increased roaring rate regardless of the severity of the threat.

In addition to roaring more frequently following the presentation of an intruder male, resident males also changed the relative intensity and gross structure of their roar sequences. Recorded roar sequences from nine different males which were followed both after a playback experiment of 1-3 intruder males and on nights with no playback were contrasted with respect to the number of roar elements and relative intensity (see General Methods, Analysis of roars, above). The average number of each roar element and the average roar intensity were calculated across all roars recorded by each male in both contexts.

Resident coalitions gave roar sequences of higher relative intensity ($P < 0.05$, $z = 2.14$, Wilcoxon Matched Pairs Signed Rank Test), and included fewer roar elements ($P = 0.002$, binomial test: Table 2) in their vocalizations after playback experiments than during follows. The number of preludes and grunts did not vary significantly with context (Table 2). When faced with an apparent intruder coalition, resident males may thus signal their aggressive intent by roaring more often, at a higher average intensity, and by modifying the gross structure of their roars.

Assessing sex and identity from roars

When faced with a roaring stranger, resident males and females will gain immediate benefits from an ability to determine the sex and identity of the individual. Both males and females will chase and attack like-sexed individuals from outside the pride (Chapter 1; McComb et al. 1994); strange males will kill cubs and strange females may co-opt territory. For an effective territorial response, residents must be able to differentiate between the roar sequences of rival and ally.

To demonstrate identification of sex by vocal cues alone, non-resident males were played the roar sequences of either one of three single females or one of five males. While resident males consistently approached strange male roar sequences (see Chapter
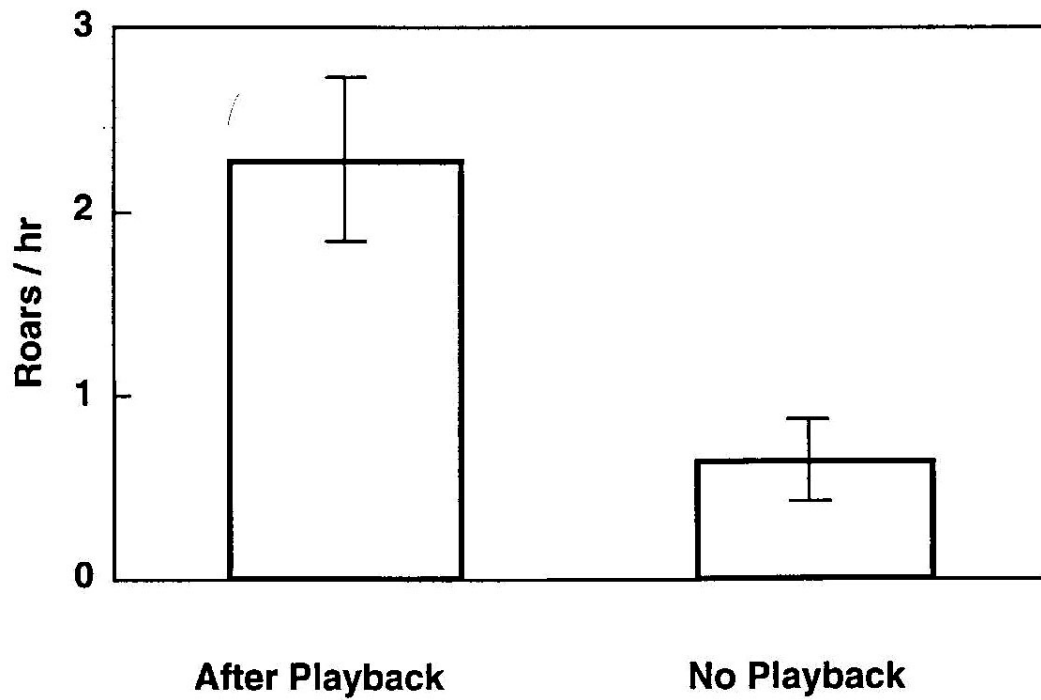
Figure 4. Rate of roaring in the hour after the playback of a simulated intruder roar sequence and during the corresponding time when no playback was performed. Resident males roared significantly more often after the presentation of an intruder roar sequence than when not: mean ± SE: simulated intruder (N = 14 coalitions), 2.27 ± 0.55 roars/hr; no-playback (N = 11), 0.64 ± 0.24; P < 0.02, z = 2.41, Mann-Whitney.

Table 2. Differences between the structures of roars when facing a simulated intruder and when not

Lion	Simulated Intruder					No Simulated Intruder				
	Recs	P	R*	G	R.I.#	Recs.	P	R	G	R.I.
CKTL	9	2.2	11.7	7.2	1.3	4	2.3	12.0	13.3	1.0
GI	5	0.0	7.5	20.0	2.1	1	0.0	10.0	14.0	2.0
JOE	5	2.2	13.0	11.8	1.0	1	6.0	13.0	6.0	2.0
L21	4	2.0	6.0	14.5	1.0	5	1.9	8.7	22.8	1.7
MOHAWK	3	2.5	7.0	30.0	1.5	1	0.0	19.0	10.0	2.0
NORM	22	2.1	8.0	7.7	1.7	36	2.3	10.1	19.3	1.8
SNAG	32	3.1	7.3	11.4	1.2	15	2.6	7.7	18.5	1.7
TWIRP1	4	2.0	6.25	13.5	1.0	27	0.9	8.9	15.1	1.7
TWIRP2	4	1.75	7.5	14.3	1.0	20	1.5	11.3	7.2	1.8

Recs: Number of recordings in each context
P: average number of "preludes" given across all roars
R: average number of "roars" given across all roars
G: average number of "grunts" given across all roars
R.I.: average relative intensity across all roars

Differences between the two contexts: * p<.002, binomial test
                                            # p<.05, Wilcoxon Rank Sum Matched Pair Test

1), non-resident males did not: of six strange-male playbacks to non-residents, three looked intently at the speaker but did not move, while the other three moved away from the speaker. In contrast, eight playbacks of single female roar sequences to non-residents elicited cautious approaches from six subjects and looks but no movement from two (Fisher's Exact Test, P = 0.009, one-tailed). Two subjects appeared in both the male and female trials, and both approached the female roar but not the male (if these two are omitted: P = 0.03, one-tailed).

Resident males in 15 coalitions were played either the roar sequences of 1-3 unfamiliar males or that of an absent coalition member. Resident males typically respond to strange-male roars in their territory by an aggressive approach (see Chapter 1), and though frequently roar within the hour following a playback (section 3) were never observed in 38 playbacks to roar concurrently with the roar sequence of a strange male. In contrast, of the five coalitions played a single, absent coalition member, four roared immediately in response, overlapping the broadcast roar sequence with their own. The fifth approached part way in a curious manner reminiscent of non-resident males approaching the roars of single females, while its other companion remained behind appearing uninterested. None of the other 11 coalitions played strange males roared with the intruder's roar sequence, and all approached the speaker aggressively (p=.003, one-tailed; Fisher's Exact Test).

DISCUSSION

Roaring in adult males appears to be a territory-specific display used only by males resident with females. Males roar in such as way as to advertise group membership and their intent to defend the territory, and appear to modify their roar sequences when confronted with simulated intruders. As lion roars can travel at least 8 km under optimal conditions (pers. obs.), efficient discrimination of vocal cues present in a roar sequence is essential to effective territorial defense as well as pride and coalition coordination. In this chapter and in Chapter 1 I have shown that those aspects of a roar sequence directly affecting its interpretation--the sex, location, identity and number of the callers--are readily determined by males.

In contrast to resident males, non-resident males remain silent. As resident males will aggressively investigate the roar sequences of strange males (Chapter 1), the cost of roaring by nomadic males to attract females or to locate coalition partners may easily be

greater than possible benefits. While Schaller (1972) believed that nomadic males would establish temporary territories from which to advertise themselves, it is likely that those males, as the ones reported on here, were seasonally resident with solitary females. In this study, two solitary females each attracted two different coalitions of males during a wet season; while thus resident, these coalitions were observed to roar, but not otherwise. However, as coalition partners greatly increase the likelihood that a coalition will gain residence (Chapter 2), nomadic males should be willing to incur a certain risk to maintain contact with partners. If roaring by nomadic males to locate absent coalition members occurs very infrequently it may have simply not been observed in the 13 nights non-resident males were followed. However, during 4 of these 13 nights I knew from previous sightings that the coalition was missing at least one male, yet even then none of these males roared. This reluctance to roar may contribute to the fragmentation of nomadic coalitions, and may require the maintenance of close visual contact between coalition members.

Role differentiation in group choruses

Duets are often organized into specific parts, each taken by a certain individual. In the lar gibbon, for example, the female of a mated pair sings a "great call" lasting about 20 s, while the male responds with a shorter coda (Raemaekers et al. 1984). As in other duetting species, this is interpreted as a territorial display directed at neighboring groups (Raemaekers & Raemaekers 1985a). While the group choruses of male lions are not so organized, contributions of the initiating and responding males are substantially different and may reflect a similar underlying function: to define the callers as a unified cooperative group. Male lions appear to time their roar sequences in order to end at approximately the same time irrespective of when each male joins the roar, and may stagger their roar elements to sound in the pauses of a companion's roar sequence. While this behavior may be selectively advantageous for other reasons, such as competition between males for female preference (see below), it will nonetheless broadcast information about group membership to listeners.

Modifying roars to announce intent

Signals associated with RHP are expected to be closely linked to body size and fighting ability (Maynard Smith 1982) because these traits often determine the outcome of competitive encounters (e.g.. Reichert 1978, Clutton-Brock et al. 1979, Thornhill

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1984). While choruses of male lions will convey RHP through advertising group size, the observation that resident males alter their roaring behavior in the presence of a simulated rival implies that the roar conveys additional information that may affect the outcome of the encounter. Increasing the rate of roaring and the intensity of roars could signal knowledge of the intruder's presence and an intent to escalate the encounter, or alternatively it could simply facilitate the assessment of coalition size by the rival group and contain no information on the likelihood of escalation. Game theory predicts that signals will rarely provide information about intentions (Caryl 1979, 1982) unless those signaling high aggression suffer costs when encountering each other (Maynard Smith 1982). Resident male lions aggressively approach the roars of strange males even when outnumbered (Chapter 1), indicating that the decision to escalate is based less on asymmetries in RHP than on the value of continued tenure in the pride, and escalated encounters can result in injury and death to the participants (Chapter 1). As such, announcing the intent to escalate will be an honest signal even if not tightly linked to RHP, for resident males will escalate despite potentially high costs even in the face of asymmetries in RHP. Limited opportunities for reproductive success in males leads to this type of "all-or-none" defense strategy (Chapters 1&2; Packer et al. 1988).

Roaring rate and intensity both reflect an increased effort by the caller, and so are logical candidates for an assessment signal. Red deer stags increase the rate at which they roar while trying to match the roaring rate of a rival (Clutton-Brock et al. 1979), and lar gibbons great call more often when challenged by playback experiments (Raemaekers & Raemaekers 1985b). However, the role of reduced numbers of high-energy roar elements after a playback is less apparent. Roar elements are likely to be energetically very costly to callers, and when giving roar sequences very frequently, such as after the presentation of an unfamiliar male roaring bout, the number of roar elements a male can give per sequence may be limited by his condition. The total number of roar elements per unit time could thus be an indication of a lion's condition. From a more mechanistic perspective, if males tend to end roar sequences approximately together, a second male joining the roar sequence earlier than usual--perhaps from greater motivation in the presence of an intruder--may prompt the initiating lion to end earlier as well. Joining a roaring bout late in the sequence of elements often seems to stimulate the initiating lion to extend the call to match endings with the responding lion. However, when considered separately from responding lions only 5 of 7 initiating males gave fewer roar elements after a playback experiment than on other nights. Alternatively, if responding lions join after the usual interval but synchronize grunts with the initiating lion, the responders may

contribute fewer roar elements to the chorus than initiating males (5/6 responding lions had fewer roars after playbacks). A combination of responding males quickly joining the lead lion, and closer synchrony between the responder and the initiator, both caused by higher motivation levels, could provide the overall result independent of other functional explanations.

Roaring and territoriality

Vocal signals that function as mechanisms for maintaining exclusive access to territory or females are expected to occur spontaneously unless prompted by the detection of a rival group (Marler 1969; Waser 1977). Male lions roar frequently (Schaller 1972; Hanby, Bygott & Packer in press), and often in the apparent absence of prior stimuli. Anecdotal evidence suggests that lions may improve their territorial signal by distributing themselves across the territory while roaring. During three resident-male follows, I knew the location of absent females and noted that the two groups joined each others' roar sequences frequently during the night, even as the males moved farther away. When the composition of neighboring groups remains fairly constant, and groups are repeatedly exposed to the vocal calls of neighbors, it may be impossible to consistently signal a deceptively large group size (cf. Harrington 1989). In such situations, it may instead be advantageous to effectively advertise the maximum group size and the extent of the territory. Roaring from separated sources is likely to increase the ability of listeners to assess group size (McComb 1992).

While male lions joined the roar sequences of their companions in a communal display (see above), they did not roar in response to the broadcast roars of unfamiliar males, but rather waited until they had failed to locate the intruders by visual means. Although in most cases it was impossible for me to determine the identity of distant roars heard during nocturnal follows, from the few occasions when they were known, lions appeared to join the distant roars of coalition and pride members but wait until well after a rival's roar had ended before responding. Raemaekers & Raemaekers (1985a) explain such avoidance of overlap in calls in lar gibbons in two ways: a group avoids overlap in order to listen to the calls of another group (perhaps to assess their group size and location), or to allow others to hear its call, or both. While the latter explanation is difficult to test, there is some suggestion that lions do listen to distant roars: males often looked in the direction of distant calls, and sometimes paused in the midst of their own roar sequence when distant lions joined it.

Other functions of roaring

While territoriality and intermale competition is the best documented function of mammalian loud calls, others undoubtedly also contribute to the maintenance of this behavior. Mate attraction has been suggested in numerous species (ungulates, Kiley 1972; hammer-headed bats, Bradbury 1977; orangutans, Mitani 1985; see also Chapter 4) but experimentally documented in only a few (e.g.. red deer stag roars, McComb 1991). More direct influences of male calls on reproduction have to my knowledge only been demonstrated in red deer (McComb 1987), but species in which males call repeatedly and spontaneously in the presence of females (such as lions, wolves, and other ungulates) are likely candidates to show this effect. Species in which ovulation is induced, such as the felids, may be especially likely candidates.

Male roar sequences may also function in intracoalition competition for female preference. There is high variance in male reproductive success in large coalitions (Packer et al. 1991), and some evidence for female preferences in mating partners (C. Packer & A.E. Pusey, personal communication). If females assess some aspect of a male's roar sequence, this could provide an alternative explanation for non-overlapping roar elements in male choruses: males may be advertising themselves to the females, or competing amongst themselves and assessing the roars of their companions. There is some evidence that females of various species prefer the call leader over followers (e.g.. frogs, Dyson & Passmore 1988; red deer, McComb 1991; katydids, Greenfield & Roizen 1993); if this were true in lions, there may be advantages to the roar initiator not gained by subsequent males that could explain differences in the structure of each type of roar. Males should in that case compete for the call leader position, especially if their roars are somehow substandard (Greenfield & Roizen 1993). Subsequent males may continue to respond because of the mutual territorial advantages of a cooperative display. These questions deserve further study.

Summary

Roaring in adult male lions is a territory-specific display used only by resident males. Roar sequences convey information on the number of lions present (chapter 1), their sex, and their identity, and lions can effectively assess this information. This assessment allows coalition members to advertise group membership even when separated, by overlapping roar sequences and altering the structure of group choruses: lions initiating group choruses include more grunts than those joining them. It also allows the avoidance of territorial males by non-resident nomads, and the formulation of an effective territorial response by residents when confronted by the roar of an unfamiliar male. Resident males roar more often and at higher relative intensities, and include fewer roar elements per roar sequence after the presentation of the roar sequence of an intruder male than during similar nights when not so challenged, indicating heightened aggressive intent and perhaps condition of the roarers. As resident lions will aggressively approach and attack intruder males (chapter 1) this is likely to be an honest signal of intention.

Efficient assessment of vocal cues to sex, number and identity of roarers also allows non-resident males to determine the number and location of roaring females and whether they are accompanied by a resident male. As non-resident males may kill the cubs of vulnerable females, they pose an immediate threat to the fitness of both resident males and females. Resident males will chase and attack alien males, and will deter their approach by advertising the coalition through group roaring. In the next chapter I examine the response of nomadic males to the roar sequences of females, and the effectiveness of females at deterring the approach of alien males through group choruses.

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