Female lions can identify potentially infanticidal males from their roars

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SUMMARY

Despite evidence from several bird, fish and mammal species that listeners can discriminate between the vocalizations of familiar and unfamiliar adult conspecifics, direct links between discriminatory abilities and fitness benefits have been difficult to identify. In free-ranging populations of African lions (*Panthera leo*), females with cubs face a substantial threat from one particular category of unfamiliar individuals: infanticidal males. Here we use playback experiments to demonstrate that females with cubs can distinguish immediately between roars from their own resident males (the fathers of the cubs) and those from unfamiliar, potentially infanticidal males. Although they remain relaxed when played roars from resident males, they immediately become agitated on hearing unfamiliar males and retreat rapidly with their cubs if the latter have reached about 4.5 months of age. These responses are not simply a function of the roarers being unfamiliar, for when played the roars of unfamiliar females, females with cubs consistently approach the loudspeaker. Furthermore, females often move towards the cubs in response to playbacks of unfamiliar males but not in response to playbacks of unfamiliar females or resident males. Our results suggest how females with cubs might, by quickly detecting and categorizing unfamiliar intruders within their territory, protect their cubs from infanticidal males and expel intruding females. Distinguishing between individuals on the basis of their vocal characteristics could therefore confer direct fitness benefits on discriminating lionesses.

1. INTRODUCTION

Experimental evidence that listeners can discriminate between the vocalizations of familiar and unfamiliar adults of their own species is widespread in the bird literature (see reviews by Ydenberg *et al.* 1988; Falls 1992), and gradually accumulating in studies of fish (Myrberg & Riggio 1985; McGregor & Westby 1992) and mammals (Waser 1977; Cheney & Seyfarth 1982, Snowden *et al.* 1983; Conner 1985; Price *et al.*, 1990; Caldwell *et al.* 1990). Attempts to determine why perceptual abilities for discriminating between adult conspecifics should have evolved have been limited by the difficulties of identifying immediate fitness benefits that efficient discriminators receive. In birds, it has been suggested that the ability to distinguish between the songs of neighbours and strangers (the 'dear enemy' effect (Fisher 1954)) benefits territorial males by enabling them to recognize opponents and so predict the outcome of contests (Ydenberg *et al.* 1988). In mammals, knowledge of conspecifics is thought to be beneficial because it improves an individual's success in competition for access to scarce resources or preferred social partners (Cheney & Seyfarth 1982, 1990). Direct links between discriminatory abilities and fitness benefits have, however, rarely been demonstrated.

An ability to discriminate between conspecifics would have obvious rewards if particular categories of individuals within the population presented a substantial and immediate threat to the future reproductive success of the discriminator. It is now well established that in a wide variety of mammals including rodents (Brooks 1984; Parmigiani *et al.* 1993), primates (Hausfater 1984; Hiraiwa Hasegawa 1993) and carnivores (Packer & Pusey 1984; Pusey & Packer 1993), males that have recently entered a new social group or area frequently kill the dependent offspring of resident females. This infanticidal behaviour accelerates the onset of oestrus in the females and thus allows the males to sire their own offspring more quickly (Hrdy 1979). As females sometimes succeed in protecting their young by resorting to evasive or defensive counterstrategies (see, for example, Pusey & Packer 1993), it would clearly benefit females if they could detect the presence of unfamiliar males at the earliest possible opportunity.

In African lions (*Panthera leo*), an estimated 27% of cub mortality is attributable to infanticide by incoming males (Pusey & Packer 1993). Infanticide by males is thought to have had marked effects on lion social behaviour and may have been an important factor selecting for sociality in females (Packer 1986; Packer *et al.* 1990). Lion prides consist of up to 18 adult females

Proc. R. Soc. Lond. B (1993) **252**, 59–64
Printed in Great Britain

59

and their dependent offspring, and the females in a pride hunt together, cooperate to defend a joint territory and communally suckle and protect their cubs (Schaller 1972; Packer *et al.* 1988). Coalitions of one to nine adult male lions compete to gain residence in prides (Bygott *et al.* 1979; Packer *et al.* 1988). Incoming males that take over a pride kill the small cubs and evict the subadult male offspring of the resident females and the subadult females that are below breeding age (Pusey & Packer 1993). The immediate effects on female reproductive success are obviously substantial. Adult females from outside the pride have also been known to kill the cubs of resident females, but recorded incidences of female infanticide are few and their effect on reproductive success difficult to access (Packer & Pusey 1984; Packer *et al.* 1988; Pusey & Packer 1993).

Females that are nursing cubs might detect the presence of unfamiliar, potentially infanticidal males by using visual, olfactory or auditory cues. As lions are active at night, however, discrimination by visual means would be effective only over very short distances. Detection through olfaction would be possible over longer distances, but odours do not usually convey accurate information on position when this is changing rapidly (Slater 1983). In contrast, the loud, low-pitched vocalizations (roars) used by lions to maintain contact with companions and advertise territory ownership (McComb *et al.* 1993; Grinnell *et al.* 1993) can be heard for upwards of 5 km (Schaller 1972) and are rich in positional information.

Unfamiliar males roaring within or close to a pride's territory would constitute a direct threat to the resident lions and their offspring (Grinnell *et al.* 1993). In this paper we describe a series of playback experiments done on a population of free-ranging lions in Serengeti National Park, Tanzania to test whether female lions with cubs can discriminate between the roars of the fathers of the cubs and those of unfamiliar, potentially infanticidal males. We also test whether nursing females can distinguish between the roars of unfamiliar males and unfamiliar females, and discuss how their behaviour in these contrasting situations might affect survival and reproductive success.

2. METHODS

(a) Study population

The lions involved in this study belonged to a population of about 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).

(b) Playback experiments

Female lions with cubs were given playbacks of: (i) roars that had been recorded from the fathers of the cubs; (ii) roars that had been recorded from unfamiliar males; and (iii) roars that had been recorded from unfamiliar females. Individuals were judged to be unfamiliar to the playback subjects if they were not typically found within 30 km of that

pride's territory; in practice, lions from the south and east of the 2000 km^2 study area were used as unfamiliar individuals in the north and west, and vice versa. All recordings had been made by using a Sennheiser MKH 816T directional microphone linked to either a Panasonic SV-250 Digital Audio Tape recorder or a Sony Professional Walkman WM-D6C. Eight different recordings of fathers, eight different recordings of unfamiliar males, and five different recordings of unfamiliar females were used in a total of 26 playbacks carried out between January 1989 and August 1991 (see Hypothesis testing).

(c) Protocol

All experiments were done when the female subjects were in a central part of their territory, had no adult males present with them, and were not feeding. To avoid habituation, playbacks to the same groups of females were always separated by at least 7 d. A single bout of roaring lasting 28–73 s (female roaring bouts, 28–55 s; male roaring bouts, 28–73 s) was played 30 min before dusk using a Panasonic SV-250 Digital Audio Tape Recorder, an ADS P120 amplifier and a Klipsch Heresy Speaker placed 200 m from the subjects (as measured on a Landrover odometer), and repeated once after 5 min if the subjects had not moved. The playback system produced peak sound pressure levels of 116 dB at 1 m. Responses of subjects were monitored for 1 h from the onset of playback by using a Sony CCD-F40 8 mm video camera and field notes. Night vision equipment was used to aid observations made after sunset.

(d) Criteria used to document responses of subjects to playback

The following criteria were used to document the responses of female subjects to playback.

1. Whether or not at least one of the females snarled. Snarling consists of opening the mouth and drawing back the lips to bare the teeth.

2. Whether or not they moved towards the cubs. Movement by females towards cubs can be movement towards the cubs themselves or towards the entrance of the den when the cubs are concealed there.

3. Whether or not they retreated from playback. In a retreat females move quickly away from the source of roars either at a run or fast walk keeping their heads low and tails down. They typically pause at intervals during the retreat and look back in the direction from which roars came. Retreats are occasionally preceded by the females taking a few initial steps ($\leqslant$ 5 m) in the direction of the loudspeaker. Females tend to bunch together both during these short advances and for retreats.

4. Whether or not they approached to the level of the loudspeaker. In an approach females typically walk tensely towards the speaker with their heads low, usually punctuating their approach with pauses and sometimes turning their heads to monitor the positions of companions during the approach (see McComb *et al.* 1993). Having reached the level of the loudspeaker they may continue on past it for anything from a few to several hundred metres, but often return subsequently either to the level of the speaker or to their original pre-playback position.

Cub behaviour was documented according to the following.

1. Whether the cubs remained relaxed or became obviously agitated (characterized by crouched posture with low carriage of head and tail) during playbacks.

2. What position they took up with respect to the adults.

(e) Hypothesis testing

(i) *Can females discriminate between roars from males that have fathered their cubs and roars from unfamiliar males?* Playbacks of fathers were given to 9 different prides and of unfamiliar males to 11 different prides. Where possible, recordings of males that were presented as fathers to their own pride were used as unfamiliar males in another part of the study area, thus 4 recordings of fathers also served as recordings of unfamiliar males. Mean number of roarers per playback was 1.56 (s.d. 0.73) for playbacks of fathers, and 1.36 (s.d. 0.67) for playbacks of unfamiliar males. A subset of experiments involved tightly controlled pairs of playbacks where the same subjects in each of seven different prides were played on separate occasions recordings of the fathers and unfamiliar males roaring. In all cases, where the 'father' recording consisted of several males roaring together this was matched with an 'unfamiliar male' recording consisting of the same number of roarers.

If females with cubs can discriminate between the roars of males that have fathered the cubs and those of unfamiliar males, and unfamiliar males represent a significant threat to the cubs' survival, then female subjects should be more likely to retreat with or defend the cubs on hearing these alien males roar.

(ii) *Can females discriminate between roars from unfamiliar males and roars from unfamiliar females?* Playbacks of unfamiliar females given to six different prides of females with cubs were compared with the 11 playbacks of unfamiliar males described above. Mean number of unfamiliar roarers per playback was 1.33 (s.d. 0.82) for playbacks of female roars and 1.36 (s.d. 0.67) for playbacks of male roars. If subjects can distinguish between these different categories of strangers, and the risk of infanticide from unfamiliar females is less than that from unfamiliar males, then female subjects should be less likely to retreat with or defend the cubs when the unfamiliar roarers are female rather than male.

(f) Statistical analyses

Simple non-parametric statistics were used in all comparisons.

3. RESULTS

(a) Playbacks of fathers against unfamiliar males

Although females remained relaxed when played recordings of their own resident males roaring, they immediately became agitated in response to playbacks of extra-pride males (figure 1). Females with cubs retreated and snarled only in response to playbacks of unfamiliar males: neither of these responses was ever observed in playbacks of fathers (table 1; Fisher's Exact Probability Test; $n = 20$, $p = 0.0003$). Whereas snarling occurred at a low frequency and the difference in the incidence of snarling to unfamiliar males against fathers was only bordering on significance (table 1; Fisher's Exact Probability Test: $n = 20$, $p = 0.0681$; but see also results of pilot tests given in table legend), retreating was a common response to playbacks of unfamiliar males. (table 1; Fisher's Exact Probability Test: $n = 20$, $p = 0.0013$). The likelihood of retreat in response to unfamiliar males was not affected by the number of adult females present at the time of playback (Fisher's Exact Probability Test; $n = 11$, $p = 0.5091$), but increased with increasing cub age (Mann–

Whitney, $U = 0$, $p = 0.008$). Examination of the data (table 2) revealed that female subjects always retreated in response to playbacks of unfamiliar males unless their cubs were less than 4.5 months old. On the three occasions when cubs were below this apparent threshold, females stood their ground rather than retreating, keeping close to cubs that were already within a metre
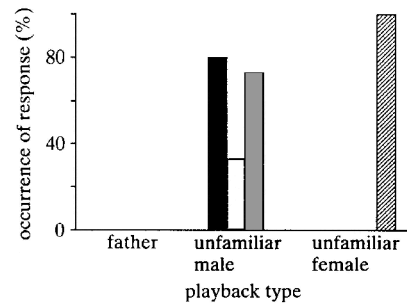

Figure 1. Female responses to playbacks of their own resident males (fathers), unfamiliar males and unfamiliar females. Responses are: move to cubs (■), snarl (□), retreat (▇) and approach (▨).

Table 1. *Occurrence of retreats, snarls and movement to cubs in response to playbacks of fathers against unfamiliar males*

response	fathers	unfamiliar males
retreat and/or snarl	0	9
no retreat and/or snarl	9	2
retreat	0	8
no retreat	9	3
snarl[a]	0	4
no snarl	9	7
movement to cubs or den	0	8
no movement to cubs or den	9	2

[a] In addition to these playbacks, pilot tests were done between 1984 and 1987 in which a single recording of an unfamiliar male was played to each of eight different prides from distances of 100–500 m. Snarling occurred in five out of these eight playbacks (and retreats in seven out of eight). When these results are included in the analysis of snarling in response to unfamiliar males against fathers (see text), a G-test on the combined data yields: $G = 5.17$, d.f. $= 1$, $p < 0.05$.

Table 2. *Retreating in response to unfamiliar males as a function of cub age*

	retreat	no retreat
mean cub age/months	14.29	4.13
	10.87	3.00 (den)
	9.67	2.68 (den)
	9.23	—
	7.87	—
	7.43	—
	4.67[a]	—

[a] In this case the pride first moved to the den to collect the cubs and then retreated with them.

Table 3. *Snarls and retreats in paired playbacks of fathers against unfamiliar males to the same prides*

pride	fathers	unfamiliar males
Gol United	none	snarl and retreat
Masai	none	snarl and retreat
Campsite	none	snarl and retreat
Masai Kopjes	none	retreat
Transect	none	retreat
Simba	none	none[a]
Barafu	none	none[a]

[a] Here mean cub age was < 4.5 months, and females moved towards the den rather than retreating.

Table 4. *Approaches to level of speaker and movement to cubs in response to playbacks of unfamiliar males against unfamiliar females*

response	unfamiliar males	unfamiliar females
approach to speaker	0	6
no approach to speaker	11	0
movement to cubs or den	8	0
no movement to cubs or den	2	6

of them (one out of three occasions) and moving closer to cubs that were further away than this (two out of three occasions). Overall, females were also more likely to move towards their cubs (or towards the entrance of a den if the cubs were concealed there) in response to playbacks of unfamiliar males than in response to playbacks of fathers (table 1; Fisher's Exact Probability Test: $n = 19$, $p = 0.0006$).

The paired playbacks of fathers against unfamiliar males to each of seven different prides confirmed the above results (table 3). Subjects were more likely to retreat and snarl in response to playbacks of unfamiliar males (Sign Test: $n = 5$ (two ties), $x = 0$, $p = 0.031$, one-tailed).

Cubs often became obviously agitated in response to playbacks of unfamiliar males (seven out of eight cases in which they were clearly visible) and led retreats in five out of eight cases; this was never observed in response to playbacks of fathers. Cubs participated in all of the retreats, remaining within a few metres of the adults throughout.

(b) Playbacks of unfamiliar males against unfamiliar females

Females with cubs behaved differently in response to playbacks of unfamiliar females than in response to unfamiliar male playbacks. When faced with unfamiliar female roars, females with cubs always approached to the level of the loudspeaker, whereas they never did this in response to playbacks of unfamiliar males (table 4; Fisher's Exact Probability Test: $n = 17$, $p = 0.0001$). Movement by females towards cubs was also confined to playbacks of unfamiliar males (table 4; Fisher's Exact Probability Test: $n = 16$, $p = 0.0035$). In fact, in playbacks of

unfamiliar females, female subjects would desert their cubs while approaching the loudspeaker if the cubs did not keep up. The cubs themselves showed no obvious signs of agitation in response to these playbacks and never attempted to retreat.

4. DISCUSSION

Adult females in lion prides that contained cubs made a clear and immediate distinction between playbacks of their own resident males and playbacks of unfamiliar males. In response to hearing their own resident males (who would present no threat to the cubs), females usually looked towards the roaring but remained relaxed and never snarled at the loudspeaker or retreated from it. In contrast, females became extremely agitated on hearing unfamiliar (potentially infanticidal) males roaring: they snarled in a third of these playbacks and retreated in more than two thirds. While there is some recent evidence in birds that females can recognize their mate's vocalizations (Wiley *et al.* 1991), we know of no previous demonstration in mammals that females can discriminate been the vocalizations of males that have fathered their offspring and those of potentially infanticidal males (but see Waser 1977).

Females' responses to playbacks of unfamiliar males suggested that they were attempting to evade the strangers rather than confront them directly. On the few occasions when they did move in the direction of the speaker this advance never took them more than 5 m and was followed by a retreat. Only the prides with the youngest cubs stood their ground. In two out of three of these non-retreats the cubs were already concealed within a den which would have afforded them some protection from incoming males but in the third they were in the open with their mother. When the cubs are very small and have limited mobility, attempts to move them while unfamiliar males are in the vicinity might actually increase the risk of infanticide. Movement by females towards cubs was common in response to playbacks of unfamiliar males but absent in response to playbacks of fathers. As a result of this, females kept close to the cubs in the potentially vulnerable period immediately after hearing unfamiliar males roaring.

Direct encounters between alien males and females with cubs are rarely observed because they usually occur at night. However, it is clear from long-term records on the study population that these encounters are often very costly for the females (Packer & Pusey 1984; Packer *et al.* 1990; Pusey & Packer 1993). In several cases where females with cubs were seen threatening or attacking alien males, the latter fought back and there are instances of females being found wounded and even dead immediately after this sort of interaction (reviewed in Pusey & Packer 1993). Furthermore, take-overs rarely occur in prides where the majority of cubs are over 6 months of age, possibly because females with older cubs can successfully avoid the incoming males and prevent a take-over (Pusey & Packer 1993). Given that females with cubs are sometimes successful in avoiding alien males and that

failure to do so can result in serious injury or death both to their cubs and themselves, retreating in response to unfamiliar male roars is likely to be the optimal strategy for females with cubs.

Although the long-term records show that the cubs of solitary females are more likely to be killed by infanticidal males than the cubs of groups of two or more females (Packer *et al.* 1990; Pusey & Packer 1993), group size had no effect on the probability that females with cubs would retreat in response to playback. Grouping by females appears to be an important counter-strategy to infanticide by males (Packer *et al.* 1990; Pusey & Packer 1993), but it is likely that the advantages of group defence would only come into effect in encounters which eventually result in a chase or fight. Groups of females should be no more likely to stand their ground than solitary individuals at a time when an immediate retreat might preclude the need for a direct interaction altogether.

It is difficult to assess whether cubs became agitated in response to playbacks of unfamiliar males because they recognized the threat from these males directly or because they were responding to signs of distress in the adult females. Their agitation was most obvious in cases where they initiated retreats but these were not the playbacks in which females snarled; if cubs were responding to anxiety in the adults then the cues involved must have been more subtle than this. Vocal recognition between mothers and offspring has been demonstrated in a variety of mammals (see, for example, Espmark 1971; Petrinovich 1974; Cheney & Seyfarth 1980; Trillmich 1982; Walser *et al.* 1982; Sieber 1986; Symmes & Biben 1985; Balcombe, 1990), although it seems to be more common for mothers to recognize the calls of their own offspring than vice versa (but see Espmark 1971; Trillmich 1982; Walser & Walters 1987). It is certainly possible that juveniles could have been selected to discriminate between the calls of fathers and those of strange males in a species where the risk of infanticide from strange males is substantial. Whether or not lion cubs possess the necessary discriminatory abilities could, however, only be ascertained by repeating the playbacks on cubs when the other members of the pride were not present.

Females with cubs never attempted to evade roaring from unfamiliar females and always approached to the level of the loudspeaker in response to these playbacks (see also McComb 1992; McComb *et al.* 1993). Movement towards cubs was also notably absent. The marked difference in response to unfamiliar male against unfamiliar female roars demonstrates that the reaction of playback subjects to unfamiliar male roars was not a function of 'unfamiliarity' per se and suggests that the two categories of stranger pose significantly different types of threat to prides with cubs. Although alien females intruding in a territory are known to show infanticidal behaviour, the limited data available suggest that infanticide by females accounts for a substantially smaller proportion of cub mortality than infanticide by males (Packer & Pusey 1984; Packer *et al.* 1988; Pusey & Packer 1993). It could also be that the risk of infanticide from female intruders becomes relatively small once they have

advertised their position. The more substantial threat under these circumstances may be a challenge for territory ownership which would be particularly serious when the pride is rearing young (see McComb *et al.* 1993). As resident females are sometimes successful in chasing away female intruders when they confront them directly (Packer *et al.* 1990; see also McComb *et al.* 1993), advancing on females that have already penetrated deep into the territory may produce the best immediate results. Although this strategy seems to involve abandoning the cubs temporarily, if successful it assures their protection in the longer term. It was notable that cubs never attempted to retreat when prides were played recordings of unfamiliar females roaring. Again, further playbacks would be necessary to determine whether the cubs were capable of distinguishing between roaring from unfamiliar females and unfamiliar males themselves or whether they were taking their lead from the adult females.

This study provides a clear example of how an ability to discriminate between social companions by using vocal cues can confer direct fitness benefits on discriminating individuals. Selection pressures of this sort could have contributed to the evolution of the highly developed skills of social cognition found in some mammal groups (Humphrey 1976; Cheney & Seyfarth 1990).

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