



Group territoriality in two populations of African lions

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Abstract. Lionesses, *Panthera leo*, in the Serengeti ecosystem, Tanzania, assess the odds of winning group-territorial contests by counting the number of opponents they hear roaring. They will approach intruders aggressively only if they outnumber them. Here the lionesses in the Serengeti are compared with another population living nearby but in strikingly different ecological circumstances. The lions of Ngorongoro Crater live at much higher densities owing to year-round availability of non-migratory prey species, but also suffer higher mortality from fighting. Playback experiments showed that lionesses in the crater differ from those in the Serengeti by approaching 'intruders' more quickly when the odds of winning are low. This increased aggression is interpreted in terms of the greater difficulty of holding a territory at high population density.

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African lions, *Panthera leo*, are well known for their gregarious life-style. They live in prides of 2–18 adult females, their dependent offspring, and one to nine males who are unrelated to the females (Schaller 1972). Females share food and nurse each other's young (Pusey & Packer 1994) but perhaps their most important shared activity is joint defence of the pride's traditional territory against other females and infanticidal males. A territory is essential for reproduction, and a single female cannot defend a territory or protect her young alone (Packer et al. 1990). Fighting entails considerable risk of injury and death (Schaller 1972), and the minimum viable pride size is two females. Females in large prides generally produce more surviving offspring (Packer et al. 1988). Whereas males always disperse, juvenile females usually remain in their natal prides. Up to one-third disperse in small groups to set up new territories next to their original pride (Pusey & Packer 1987).

Male and female lions advertise their territories by roaring, and use the number of roars they hear to gauge the strength of the opposition. A recent series of studies have made use of this trait to simulate territorial intrusions of varying intensity by playing back the roars of different numbers of

'intruders'. In reaction to such 'invasions' from their own sex, females are more likely to respond if they outnumber the opposition (McComb et al. 1994) whereas males tend to advance towards the enemy regardless of the odds (Grinnell et al. 1995). Recently, females were shown to have a variety of strategies ranging from cooperative territorial defence to lagging behind and letting others carry the risks of fighting (Heinsohn & Packer 1995). Juvenile females become progressively more likely to join the adults in defence as they mature, but are more sensitive than adults to the odds of winning (Heinsohn et al. 1996).

Pride structure, home range size and population density all correlate with food availability, especially the period of lowest prey biomass in the course of a year (the 'lean' season, Van Orsdol et al. 1985). Whereas both pride size and density are positively correlated with lean season biomass, range size is inversely correlated with this measure. Despite such clear variation between populations, only one study has attempted to compare the behaviour of lions living in different habitats (Hanby et al. 1995). Here I compare the territorial behaviour of females in two adjacent reserves in Tanzania with markedly different ecological and demographic conditions. Whereas the Ngorongoro Crater has large numbers of non-migratory prey species and supports the highest density of lions in Africa (Van Orsdol et al. 1985), lions in the Serengeti National Park live at lower

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densities owing to periods of near famine caused by the large-scale migration of their prey species (Packer et al. 1988).

I make use of playback experiments to gauge the territorial behaviour of females in both the Serengeti and the Ngorongoro Crater. I hypothesize that a high density leads to greater intruder pressure and competition for space in the crater, and that invasion of like-sexed strangers may elicit a stronger territorial response from established prides.

METHODS

Study Areas and Populations

The Ngorongoro Crater is a large volcanic caldera that contains one of Africa's highest densities of lions (Van Orsdol et al. 1985). The high density is thought to be caused by large populations of non-migratory prey including wildebeest, *Connochaetes taurinus*, zebra, *Equus burchelli*, and African buffalo, *Synceros caffer* (Van Orsdol et al. 1985; Hanby et al. 1995). The crater is essentially an island of prime habitat in which prides produce large numbers of young, many of which emigrate (Pusey & Packer 1987), but in which no immigration from surrounding areas has occurred for at least 30 years (Packer et al. 1991). Although survival of young lions is generally higher in the crater, the high population density also leads to increased fighting and higher adult mortality (Packer et al. 1988).

In contrast, the Serengeti ecosystem is defined by the seasonal migration of its large herbivores. The wildebeest, zebra and gazelle, *Gazella* spp., leave the northern woodlands in vast numbers to graze on the eastern plains during the rainy season (November–May) each year (McNaughton 1979), but these areas have little prey during the remaining months. Prides on the plains have large poorly defined territories as they are forced to wander great distances to find sufficient prey, whereas those in the woodlands and on the woodland edge have smaller territories with more constant supplies of food (Packer et al. 1988).

The study population from the Ngorongoro Crater consists of seven prides living at a density of approximately one lion per 2.5 km² (Hanby et al. 1995), whereas the 2000-km² study area of the Serengeti National Park has 17 prides at approximately one lion per 10 km² (Packer et al.

1991). Both populations have been monitored continuously for over 20 years (Schaller 1972; Hanby & Bygott 1979; Packer et al. 1988, 1991), based on recognition of individuals. For details of individual recognition and other monitoring methods see Packer et al. (1988). Here I use the responses to playbacks of nine prides, six from the Serengeti and three from Ngorongoro. All prides had at least two adult females and 2–17 juveniles of either sex. Although this study compares the territorial behaviour of the two populations occurring at different densities and ecological circumstances, it is not possible to isolate with certainty any factor (e.g. density) as the only cause of differences between the populations.

Playback of Roars

Playback techniques followed those of McComb et al. (1994). Briefly, from mid-1991 to mid-1993 I simulated intrusions into the pride's territory by playing from a speaker the roars of either one or three lionesses simultaneously. The individuals played were randomized with respect to identity and were always unlikely to be known by the pride (e.g. recorded from the opposite side of the study area). In all cases, playbacks were conducted between 1 h and 30 min before dusk, and the speaker was placed at 200 m from the pride. Playbacks were not conducted if (1) the adult males were present, (2) the pride had any suckling cubs, or (3) any members of the pride were emaciated or had obvious wounds. See Heinsohn & Packer (1995) for further details of playback methods.

The basic data consisted of the binary response of 'yes' or 'no' describing whether any members of the pride responded to the playback by moving forward and reaching at least the half-way point between the pride's original position and the speaker. This response was modelled in a logistic regression using the 'odds' of winning the contest (i.e. the number of adult females present divided by the number of recorded intruders), as the major independent variable. I followed McComb et al. (1994) by not including juveniles (pre-reproductive individuals aged 8–42 months) in the calculation of 'odds', as in their study juveniles had a smaller effect than adults, and in this study they had no effect. I use the cut-off age of 42 months as a separate analysis has shown that individuals of that age are still less likely to

approach intruders than older individuals (Heinsohn et al. 1996). Other factors included in the model were habitat (i.e. two study sites), pride identity, the mean age of adults and the mean age of juveniles. I calculated whether including a factor significantly improved the fit of the logistic regression using the change in deviance, which approximates a chi-square distribution (Dobson 1983).

The second response variable used was the mean latency of all adult females (>42 months) present for the playback to reach the half-way point (100 m), giving a single value per playback. Females were considered to have failed to respond if they had not moved past the half-way point 1 h after the playback. In these cases ($N=6$), I calculated mean latency for all of the individuals that had crossed the half-way point. Mean latency was modelled in a multiple regression using the same variables as above.

RESULTS

It was necessary to exclude one pride (the K2s, see below) leaving eight prides for analysis. Overall I conducted 110 playbacks to these prides, of which 94 elicited an approach to the speaker. At least some individuals in each pride responded to every playback conducted in the crater ($N=27$), whereas the entire pride failed to respond on 16 occasions in the Serengeti ($N=83$). However, this difference was not significant in the logistic regression model ($\chi^2_1=1.5$; NS). Overall, the likelihood of response was dependent on the odds ($\chi^2_1=23.6$, $P<0.001$), but not on any other variable tested (pride identity, $\chi^2_1=0.1$; mean age of adults, $\chi^2_1=0.8$; and the mean age of juveniles, $\chi^2_1=0.6$, all NS). Whereas McComb et al. (1994) showed that the number of juveniles present had a positive effect on the likelihood of the pride responding, there was no such effect in this study ($\chi^2_1=1.2$, NS).

The Serengeti K2s were excluded because of the complete incompatibility of their behaviour with that of other prides. They not only failed to approach the speaker in any of the eight playbacks conducted to them, but actively retreated each time to more than 500 m upon hearing the roars. This pride was the offshoot of a larger pride, did not have a well-defined territory, and wandered over an extended home range. After breeding successfully, its two adult females and

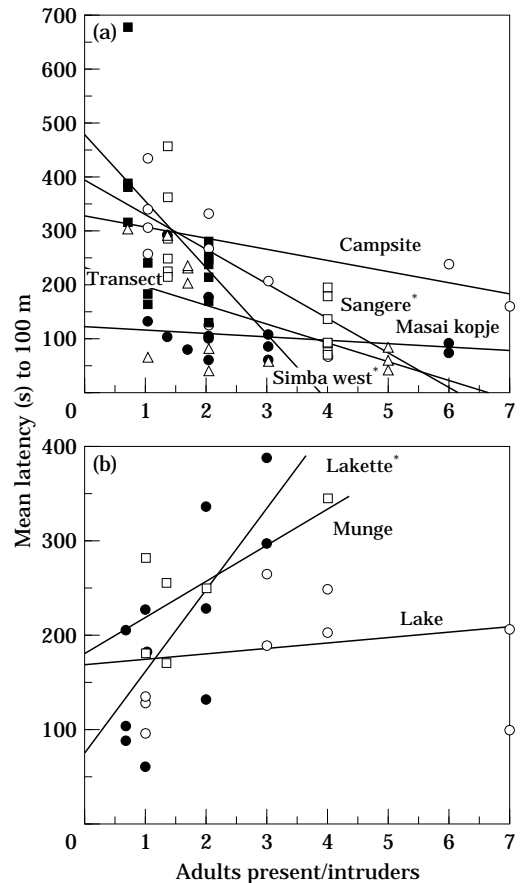


Figure 1. Regression of mean latency (s) of individuals in each pride to reach the half-way point (100 m) to the speaker. (a) The five Serengeti prides. Those with slopes significantly different from zero (P -values given in text) are marked with an asterisk. Campsites (\circ), slope = -20.5 ; Sangere (\square), slope = -69.5 ; Masai kopje (\bullet), slope = -6.5 ; Transect (\triangle), slope = -35.5 ; Simba west (\blacksquare), slope = -126.5 . (b) The three Ngorongoro Crater prides. Lakette (\bullet), slope = 91.5 ; Munge (\square), slope = 41.5 ; Lake (\circ), slope = 22.5 .

three juveniles have since disappeared from the study area one by one, and are presumed dead. The behaviour of the K2s contrasts with a similar pride in the Serengeti, the Simba wests, which were offshoots from the larger Simba pride. They had two adult females and three subadults and approached intruders even when their adults were outnumbered three to two (Fig. 1). Another small pride in the crater, the Lakettes (three adults and three juveniles), always responded and showed

some of the quickest responses to playbacks (see below).

In the regression model of mean latency to reach the half-way point, latency was shown to depend on odds, with slopes varying with 'pride' ($F_{7,85}=8.5$, $P<0.001$). When added to the model in the absence of 'pride', 'habitat type' had the same effect ($F_{1,92}=27.9$, $P<0.001$). Inclusion of the eight different prides accounted for 61% of the variance whereas habitat type accounted for only 35%; it is clear that 'pride' contained all the information given by 'habitat type'. Three prides, two from the Serengeti and one from the crater, had slopes significantly different from zero (Sangere, $P=0.0006$; Simba west, $P=0.0006$; Lakette, $P=0.004$). Serengeti lionesses approached the speaker more slowly and cautiously when the odds of winning were lower, whereas crater prides tended to respond either at the same pace or even more quickly at low odds (Fig. 1). Slopes differed significantly between the two study sites (Mann-Whitney $U=0$, $N_1=5$, $N_2=3$, $P=0.025$).

DISCUSSION

McComb et al. (1994) showed that lionesses assess the odds of winning a territorial contest by comparing the number of opponents they hear roaring with the number of their own pride present. In the Serengeti they tend only to approach like-sexed intruders if they clearly outnumber them, and approach more cautiously when the odds are lower. Because fighting between lionesses often results in injury or even death (Schaller 1972; Packer et al. 1988), such numerical assessment skills may allow individuals to avoid costly, unwinnable contests. However, the extent to which individuals are prepared to fight for resources depends on their scarcity and distribution, and the extent of competition from other individuals (Davies & Houston 1984). Whereas McComb et al.'s study was conducted entirely in the Serengeti, I compared the Serengeti population with one living at a much higher density and in different ecological circumstances.

Although not significantly different, there were 16 ($N=83$) cases when the pride failed to approach the simulated intruders in the Serengeti, whereas all prides always responded ($N=27$) in the crater. The likelihood of approaching intruders increased

significantly with odds, and prides in this study often approached at lower odds than in McComb et al.'s (1994) study (e.g. at 3:3 and 1:1). This may be because all prides had 2–17 juveniles, whereas many of those in McComb et al.'s (1994) study had none. Interestingly, there was no effect in this study of the number of juveniles present; any such effect may have been masked by the lack of prides with one or no juveniles. Juveniles become progressively more likely to respond to territorial intruders as they mature, but their behaviour remains dependent on the ratio of adult defenders to intruders (Heinsohn et al. 1996). They increase the pride's likelihood of responding, but apparently not in proportion to their numbers.

In contrast, a clear difference emerges in the speed at which individuals approached intruders. Whereas Serengeti lionesses tended to be more cautious in their approach when the odds were low (i.e. all slopes negative in Fig. 1), crater lionesses approached either at the same speed in all circumstances, or even faster when the odds were low (positive slopes, Fig. 1). It seems those in the Serengeti approach intruders tentatively when outnumbered whereas at least some in the crater do the opposite.

The crater is characterized by populations of large prey species including wildebeest and zebra that rarely leave the crater. This contrasts with the 'feast' and 'famine' conditions caused by large-scale migration of the major herbivores in the Serengeti (McNaughton 1979). Although there are seasonal movements of grazing herds within the crater, the seven prides have small territories centred around permanent water sources which serve to attract prey even in the dry season (Packer et al. 1988). The crater population crashed to only 10–15 animals in the early 1960s because of a biting fly, *Stomoxys calcitrans*, epidemic but increased to its present level by 1975 (Packer et al. 1991). Interestingly, no lions from outside the crater have managed to take up residence there over the past 30 years; this may be due to the larger body size of crater lions (C. Packer, unpublished data) and the surplus of 'floaters' from the crater ready to fill vacancies (Hanby & Bygott 1987).

Since 1981, only one break-away group of crater females has managed to establish a territory and breed successfully, reflecting the crowding of many prides into a small area and extreme competition for space. This compares with the

Serengeti where four out of 15 territories presently being monitored have been established since 1981. The threat of losing essential, difficult-to-acquire territory may be why some crater lionesses respond even more quickly when the odds are low (Fig. 1). Such preparedness to escalate fighting has been shown in other studies where resources are highly contested (e.g. Riechert 1986). The results of failing to challenge intruders are well illustrated by the K2 pride of the Serengeti. This pride unexpectedly failed to approach the speaker in any of the playbacks ($N=8$), even when the adults outnumbered the opposition two to one. Instead they retreated immediately upon hearing the roars. This pride died out gradually over the course of a year, starting with the juvenile female and followed by the adult females, probably from aggression from other prides. A conceptually similar argument has also been used for male lions which appear to have little to lose by challenging intruders when outnumbered. Males have only one chance in their entire lifetimes for reproductive success, and seem prepared to fight for control of the pride regardless of the odds (Grinnell et al. 1995).

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