Development of cooperative territoriality in juvenile lions

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SUMMARY

African lions, *Panthera leo*, engage in many cooperative activities including hunting, care of young, and group territoriality, but the contribution of juvenile lions to these activities has never been documented. Here we present experimental evidence that juvenile lionesses make a gradual transition to group-territorial defence between weaning (8 months) and sexual maturity (42 months). When challenged by simulated intruders played from a loud-speaker, juvenile females (but not males) become progressively more likely to join the adult females in territorial defence with age, and their behaviour is affected by both the number of defending adults and the number of intruders. We interpret the ability of juveniles to assess relative numbers as an adaptation for assessing the risk of territorial conflict according to their own fighting ability, and the ability of their pride to successfully defend the territory. The difference between the sexes reflects the greater value of the natal territory to philopatric females. Adult females display a variety of strategies when defending the territory, including unconditional and conditional forms of cooperation. We show here that individuals display the rudiments of these strategies as juveniles.

1. INTRODUCTION

In cooperative societies, individuals may forgo independent reproduction and help others to breed (Brown 1987; Jennions & MacDonald 1994), or they may reproduce alongside others and enjoy their active and passive help (Smuts *et al.* 1987; Emlen 1991; Pusey & Packer 1994). Individuals born into either scenario may develop cooperative behaviour at an early age, but its ontogeny is poorly understood. Recently, the costs and benefits that trade off to produce cooperative behaviour in young individuals have received more attention. For example, the decision to cooperate may be influenced by parental manipulation (see, for example, Emlen & Wrege 1992), parental enforcement (Mulder & Langmore 1993), or other social circumstances such as how many individuals contribute to the corporate group effort (see, for example, Heinsohn & Cockburn 1994). In the latter case, young individuals may only decide to cooperate if their contribution produces benefits large enough to overcome the costs associated with their own limited abilities. Despite a growing body of literature that explicitly deals with the behavioural ecology of juvenile animals (Altmann 1991; Heinsohn 1991; Pagel & Harvey 1993; Pereira & Fairbanks 1993), more attention needs to be focused on if, when, and how juveniles decide to cooperate.

We studied the gradual development of cooperative territorial behaviour in juvenile lions, *Panthera leo*, from weaning to sexual maturity (approximately 8–42 months, Packer *et al.* 1988). Lions are unusual among cats in having a social system based on permanent association of female family members. A 'pride' of lions consists of between two and 18 related females, their cubs, and their weaned juveniles up to the age of 42 months (Schaller 1972; Packer *et al.* 1990). Female lions share food and nurse each other's young, but perhaps their most important form of cooperation is group defence of the pride's traditional territory from infanticidal males and other females. Fighting is a common cause of injury and death, especially for small prides and solitary animals (Schaller 1972; Packer *et al.* 1990). Juveniles develop from being totally dependent on the females for prey and territorial protection (Packer *et al.* 1988; McComb *et al.* 1994), to contributing in large measure to both activities. More loosely associated with the pride is a coalition of one to nine males, unrelated to the females, that defend access to the females and their offspring for two to three years before being evicted by other males (Grinnell *et al.* 1995). Females usually stay in their natal pride, but young males disperse at 2–4 years of age, often with their cohort mates, in a quest to take over a new pride (Pusey & Packer 1987).

Territorial intrusions can be simulated by playback of recorded roars, and this technique has been used to elicit cooperative defence in like-sexed adults (McComb *et al.* 1994; Grinnell *et al.* 1995). Playbacks have shown that lions can distinguish pridemates from strangers, and assess the odds of winning a territorial contest by comparing the number of intruders with the

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number of defenders (McComb *et al.* 1993; McComb *et al.* 1994; Grinnell *et al.* 1995). Recently, Heinsohn & Packer (1995) demonstrated that adult lionesses display an unexpected variety of behavioural strategies when defending the group territory. Most cooperate in defence unconditionally, but others only contribute when the odds of winning would otherwise be low. Some females 'cheat' by consistently lagging behind and letting their companions bear the risks of fighting, and a few lag even further when their help is most needed. These strategies are highly consistent within individuals. Here we show that the tendency by some individuals to lag behind emerges when they are juveniles, along with the ability to assess numbers during territorial conflict and calculate the risk of injury. Our study contrasts the territorial development of males and females, and emphasises the juvenile period as the starting point for adult behavioural strategies.

2. METHODS

We conducted our study in the Serengeti National Park and Ngorongoro Crater, Tanzania using ten prides in which all lions were individually recognized (Packer *et al.* 1988). Most lions are born in litters of one to four cubs (Packer & Pusey 1995), and as two or more females may give birth synchronously, cohorts may contain more than 20 juveniles. In this study, cohorts ranged from two to 17 individuals, with varying sex ratios. We consider the juvenile period to cover the period from weaning (8 months) to sexual maturity at approximately three-and-a-half-years-old.

We simulated intrusions of strange female lions into the pride's territory by playing from a speaker the roars of either one or three lionesses simultaneously (McComb *et al.* 1994). The speaker was placed 200 m from the pride and was operated by remote control. Between six and 15 of these playbacks (total = 114) were conducted to each pride over a 24 month period. For details of playback methods see Heinsohn & Packer (1995).

Playbacks were not conducted if: (i) individuals had obvious wounds, as this might affect their willingness to challenge intruders; (ii) adult males were present (males often spend time elsewhere in the territory), as any approach by resident males may be a sexual rather than territorial response; and (iii) the pride had any cubs that were still suckling (less than 8-months-old), as their presence may affect the mothers' motivation to defend the territory (McComb *et al.* 1994).

The response of most adult lionesses upon hearing the roars was to look in the direction of the speaker, and then approach the speaker at walking pace. Those in the lead adopted a tense posture with head held low, and the approach of the leading individuals was often punctuated by pauses. Adults are more likely to approach the speaker if they outnumber the 'intruders (McComb *et al.* 1994). As our aim was to elicit a territorial response from the pride, the number of roars played only rarely exceeded the number of defending adults. The juveniles usually looked up at the speaker immediately upon hearing the roar, but did not necessarily approach with the adults. If they did approach, they virtually always lagged behind the adults. One pride (the K2's) that included two adult females, one juvenile female, and two juvenile males always ($n = 8$) retreated upon hearing the roars. This pride was a small offshoot from a larger pride, wandered over an extended range, and did not defend a well-defined territory. Their responses are not included in any of the analyses presented here because of the striking contrast between their behaviour and that of other prides. For the remaining nine prides, two measures are used for analysis: whether a juvenile approached with the pride and the order amongst the juveniles in which it approached the speaker.

(*a*) *Whether juveniles approach intruders*

The results of each playback where adults approached the speaker (101 out of 114 playbacks) were reduced to two values, the proportion of the male and female sub-adults which also approached the speaker. In most cases, either all or none of the juveniles responded, but some values ranged between zero and one. As the values for males and females in each playback may not have been statistically independent, we chose at random either the value for males or females, so that only one value per playback was used in the analysis. These were used as the response variable in a logistic regression done in GENSTAT (GENSTAT 5 Committee 1987). A factor 'pride' was incorporated in each analysis to control for any variation specifically associated with each pride. Other factors hypothesised to influence juvenile behaviour were then added sequentially, these included: (i) whether adult females were present; (ii) the number of adult females; (iii) the number of intruders; (iv) sex of juveniles; (v) mean age of juveniles; (vi) the number of juveniles present; and (vii) all interactions between these variables. It should be noted that 'pride' is independent of 'number of adults' and 'number of juveniles' caused by the fission–fusion nature of lion sociality, in which pride members are found in constantly changing combinations.

(*b*) *The position of juveniles in the group response*

Those juveniles that approached the speaker usually lagged behind the adults in single file or in pairs or small groups. The fission–fusion nature of lion prides meant that differing numbers of juveniles and adults were observed on different occasions. The order in which juveniles approached intruders was standardized to a value (rank) between 1 (first juvenile) and -1 (last juvenile) to account for this variation. Sample sizes where juveniles responded to the playback and could thus be assigned ranks ranged from six to 12. These measures were used to examine individual behaviour over the study period in two ways. First, as individual responses were approximately normally distributed, differences between individuals in their preferred positions within each pride were tested using ANOVA. Second, the consistency of individuals over the study period was tested by calculating the correlation between their first and last recorded standardized rank. This last test is important as it ensures there were no major deviations in individual behaviour at the end of the study period when the individuals were older.

3. RESULTS

(*a*) *Juvenile approach*

The willingness of juveniles to approach intruders depends on a range of factors. These were: pride ($\chi^2_8 = 157.7$, $p < 0.001$), whether adults were present ($\chi^2_1 = 39.3$, $p < 0.001$), sex ($\chi^2_1 = 43.4$, $p < 0.001$), mean age*sex ($\chi^2_1 = 9.9$, $p < 0.005$), number of adults ($\chi^2_1 = 33.0$, $p < 0.001$), number of intruders ($\chi^2_1 = 209.0$, $p < 0.001$), and number of adults*age ($\chi^2_1 = 4.7$, $p < 0.05$).

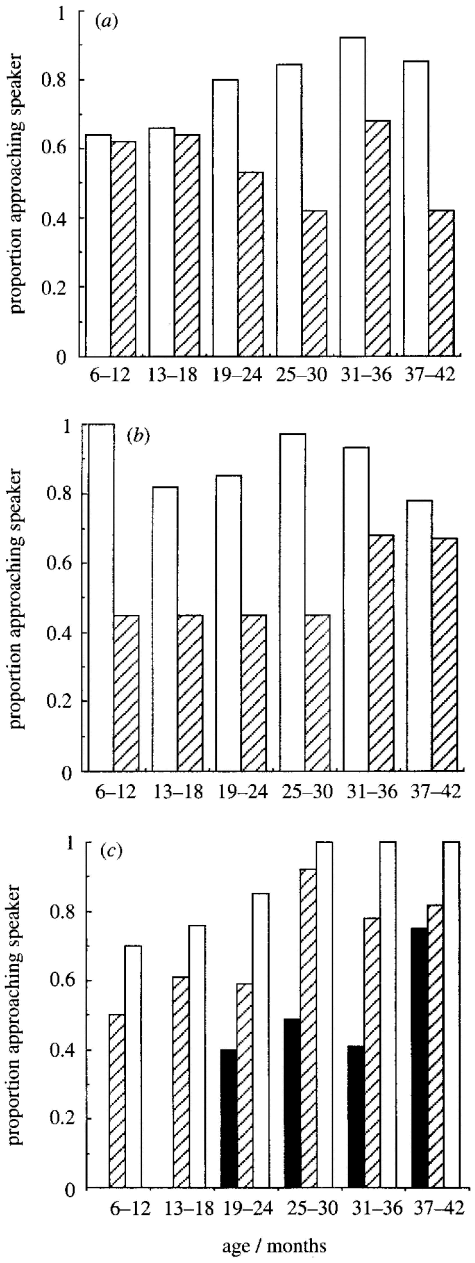

Figure 1. The proportion of juveniles that approached the speaker with the adults ($n = 101$) plotted over age (months). (*a*) The differing proportions for males (hatched bars) and females (open bars). (*b*) The differing proportions when the pride is faced with either one (open bars) or three (hatched bars) intruders. (*c*) The differing proportions when there are zero adults (solid bars), one-three adults (hatched bars), or four to seven adults (open bars) present.

p values were calculated using the change in deviance (which approximates a χ^2 distribution, Dobson 1983) after each factor was added to the model.

The effects of sex, number of intruders and number of adults present are presented in figure 1. Whereas the

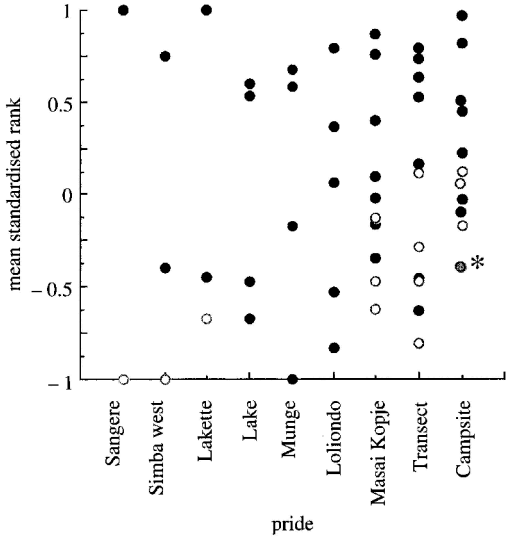

Figure 2. The distribution of mean standardized ranks of juveniles in nine prides. Filled circles are females, and open circles are males. Because of incomplete information, only ten individuals in a cohort of 17 juveniles are shown for the Campsite pride. A single mean for all seven remaining males is shown as one data point indicated by an asterisk.

males' response was not dependent on age, juvenile females were more likely to approach intruders as they approached maturity (figure 1*a*). Juveniles were sensitive to both the number of intruders and adult defenders. They were less likely to approach when there were more intruders (figure 1*b*), and more likely when there were more adults in their own pride (figure 1*c*). When there were no adults present, 40–50% of juveniles between 19 and 36-months-old approached the speaker, whereas juveniles between 37 and 42-months-old approached on over 70% of occasions. Juveniles less than 18-months-old were never found without adults, so no data are available for these categories.

(*b*) *Position of juveniles*

There was a high correlation between the standardized rank of juveniles in the first and last playback in which they participated ($r = 0.706$, $p < 0.001$), indicating consistency of individual positions during the response to playbacks. The length of time between these playbacks ranged from six to 24 months. The mean standardized ranks (taken over whole study) differed significantly between individual juveniles in all nine prides ($n = 38$ females, 21 males, $p < 0.001$ for all prides, figure 2), where the mean age for the various cohorts used ranged from 11.3 to 39.6 months. Thus the approach to the speaker is non-random, and at least some individuals prefer to remain closer to the front or to the back of the group response. Where the cohort was of mixed sex, juvenile females were more likely to lead and males were more likely to lag (see figure 2).

4. DISCUSSION

McComb *et al.* (1994) have shown that adult lionesses weigh the odds of winning a contest, and only approach female intruders if they outnumber them. They relate the ability to assess relative numbers to the resource holding power of a pride, and suggest it reduces injury from fighting unwinnable contests. Juvenile lions also appear capable of judging the relative strength of their own pride versus the enemy, and are more likely to approach if the 'odds' are favourable (figure 1). Thus the ability to assess relative numbers is a trait first displayed by juveniles probably as a mechanism for judging the danger of staying close to the adults during conflict situations.

The response of young juveniles to intruders is unlikely to be purely aggressive as lions do not reach their full body size and physical fighting potential until about 30–36-months-old (C. Packer, unpublished data). Even juveniles less than 12-months-old have a 50–70% likelihood of approaching intruders with the adults (figure 1*a*). At that age they may choose to stay close to adults for greater protection, or because they are dependent on them for food, and cannot afford to become separated. The profile when adults are not present (figure 1*c*) is the most conservative measure of the true territorial response, as these juveniles assume the risks of injury from fighting (Schaller 1972; Heinsohn & Packer 1995) without adult protection. As juveniles assume full body size, the benefits of directly challenging intruders gradually overcome the risks, and the earliest expression of territoriality would be expected when juveniles are both isolated from the adults and facing territorial incursions. For example, one cohort of five juvenile females from the Loliondo pride spent most of the study period away from the adults on the edge of the natal territory. From the age of 27 months they responded to every playback in which they outnumbered the enemy. Figure 1*c* shows that juveniles aged 19–24 months and unaccompanied by adults have a 40% likelihood of approaching intruders. This value reaches over 70% by the age of 37–42 months. In this study, juveniles less than 18-months-old were never found without adults, so it is not possible to evaluate their response to intruders at this age.

Juvenile males differ from juvenile females in their response to intrusion in two ways. Whereas females become more likely to respond with age, males do not (figure 1*a*), and when males do respond they are most likely to be at the back of the group response (figure 2). If willingness to fight were determined by body size alone, males would join in sooner than females as they grow more quickly (Smuts *et al.* 1978). Similarly it is unlikely that juvenile males fail to recognize the stimulus as adult males are known to respond to female roars (Schaller 1972; Grinnell & McComb 1996). Clearly, juvenile females are more motivated to respond to intrusions by extra-pride females.

Female lions usually remain in their natal pride for their entire lives, but males over 3-years-old disperse, often with others from their cohort (Pusey & Packer 1987; Grinnell *et al.* 1995). After a period of nomadism, they attempt to take over another pride by evicting the resident males. Thus the first real need for aggression occurs after they have left their natal pride, in the context of fighting directly for mating opportunities. Females, in contrast, inherit a traditional pride territory (Packer *et al.* 1988). As this is essential for reproduction, they gain direct benefits from contributing to group territoriality as soon as they are capable. Indeed, the mere presence of juveniles has been shown to have a positive effect on the likelihood of adults approaching intruders (McComb *et al.* 1994).

In the best studied social mammals, the primates, juveniles of the philopatric sex often participate in the adult activities of their group. Although practice is probably beneficial, it is also likely that they secure resources and social bonds (Walters 1987). When females are philopatric (eg. macaques, Silk *et al.* 1981; baboons, Periera & Altmann 1985; vervet monkeys, Fairbanks & McGuire 1985), they participate in adult activities such as grooming and infant handling from an early age. However, juvenile males in these species become progressively more peripheral to the social group. Whereas the bonds juvenile females form with others may confer a head-start for adulthood, males presumably have less to gain from socialising with peers and adults that they will eventually leave. In contrast, when males are philopatric (eg. chimpanzees), they maintain higher levels of contact with the adults in their communities (Pusey 1983). Thus juvenile lions appear to be consistent with the trend in primates, with only the philopatric females investing heavily in the defence of their social group.

Perhaps the most intriguing aspect of the data presented here is that juvenile females from 6 to 42-months-old show consistent preferences for position during group territorial responses (figure 2), and that these preferences persist over long periods of the juvenile phase. Thus juveniles display leading and lagging behaviour similar to that shown for adults (Heinsohn & Packer 1995). A shy–bold continuum has been identified for many other species (Wilson *et al.* 1994), even for very young animals (see, for example, Fairbanks & McGuire 1993), and is manifested as the propensity to take risks such as approaching novel stimuli. In humans, these basic differences are referred to as temperament. They have a genetic basis, and although modified according to circumstances, show significant consistency through early childhood (Kagan 1988). Thus the position of juveniles during playbacks may reflect differences in temperament, with bolder individuals at the front. However, there is no correlation between the preferred positions of mothers and daughters (Heinsohn & Packer 1995) suggesting that other non-inherited factors influence development of such behaviour.

This study identifies various factors which affect the likelihood of a territorial response from juvenile lions. Sex and basic personality types, possibly embedded genetically, explain some of the variation. However, developmental plasticity to social conditions such as pride size and risk from intruders may also influence territorial behaviour. Thus, if the various styles of cooperation amongst adult females form a mixed ESS

as suggested by Heinsohn & Packer (1995), variation in temperament and social environment may serve as the substrate for development of optimal adult strategies.

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