Infanticide and expulsion of females in a cooperative mammal

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In cooperative groups of suricates (*Suricata suricatta*), helpers of both sexes assist breeding adults in defending and feeding pups, and survival rises in larger groups. Despite this, dominant breeding females expel subordinate females from the group in the latter half of their (own) pregnancy, apparently because adult females sometimes kill their pups. Some of the females that have been expelled are allowed to rejoin the group soon after the dominant female's pups are born and subsequently assist in rearing the pups. Female helpers initially resist expulsion and repeatedly attempt to return to their natal group, indicating that it is unlikely that dominant females need to grant them reproductive concessions to retain them in the group.

Keywords: dispersal; cooperative breeding; reproductive skew

1. INTRODUCTION

Since systematic infanticide was first described in Hanuman langurs, *Presbytis entellus*, by Sugiyama (1965), it has proved to be common in a wide range of social mammals, including other primates (Hrdy 1977; Abbott 1984; Hiraiwa-Hasegawa & Hiraiwa 1994) rodents (Sherman 1981; Hoogland 1994; Elwood & Kennedy 1994) and carnivores (Packer & Pusey 1984). Three principal categories of infanticide account for most known cases in natural populations (Hrdy 1979): infanticide by members of other social groups (Bygott 1972; Hiraiwa-Hasegawa & Hiraiwa 1994); infanticide by male immigrants unrelated to the juveniles or to the infants that they kill (Hrdy 1977; Packer & Pusey 1984); and infanticide by female competitors (Sherman 1981; Abbott 1984; Digby 1994). Infanticide commonly represents a major source of juvenile mortality (Sherman 1981; Packer & Pusey 1983) and females have evolved a range of strategies that reduce its frequency, including delaying oestrus after the arrival of new immigrants, abortion, temporary absence from the group and cooperative defence of young (Hrdy 1979; Packer & Pusey 1983).

In this paper, we document the incidence of infanticide in a cooperative mongoose, *Suricata suricatta*, and describe a novel strategy taken by breeding females to reduce the risk of infanticide to their pups. In suricates, multiple males and multiple females live together in territorial groups of 5–25 in the arid areas of southern Africa (Doolan & Macdonald 1996). In most groups, a single female is responsible for over 75% of all breeding attempts, although multiple females may conceive and carry pups until birth. Dominant females usually attempt to breed two or three times per year, whereas sub-

ordinates rarely do so more than once per year (Clutton-Brock *et al*. 1999*a*). Helpers are responsible for most aspects of parental care (including babysitting, carrying and feeding pups) and parents contribute relatively little to some cooperative activities (Clutton-Brock *et al*. 1998). Where predators are abundant, survival rises in relation to the number of helpers (Clutton-Brock *et al*. 1999*a,b*), as in dwarf mongooses (Rood 1990). In this paper, we initially review evidence of infanticide by females and subsequently describe how breeding females drive other mature females (including their sisters and daughters) out of the group during the later stages of their own pregnancy.

2. METHODS

Reproduction, survival and behaviour were monitored in 28 groups of suricates living in the southern Kalahari between February 1993 and April 1998 (Clutton-Brock *et al*. 1998, 1999*b*). Groups had an approximately equal sex ratio and consisted of matrilineal relatives born in the group and between one and four unrelated immigrant males. In each group, one male and one female were socially dominant to all other group members. Dominant females displaced all other group members when artificial food (hard-boiled egg) was provided; their rate of marking the substrate with cheek or anal glands was around ten times higher than that of other females; they were the only females that regularly became pregnant; they usually conceived earlier in the breeding season than other females; and they were rarely involved in babysitting or guarding (Clutton-Brock *et al*. 1998). Individuals were classified as pups from birth to three months; as juveniles from three to six months; as sub-adults from six to twelve months; and as adults once they were a year old (Clutton-Brock *et al*. 1999*a,b*).

Groups occupied partly overlapping ranges of 2–5 km^2 of dry river-bed, dunes and dune slacks covered with sparse perennial grasses, shrubs and occasional trees (Leistner & Werger 1973; Clutton-Brock *et al.* 1998). Both study areas experienced a hot, wet summer (October–April), followed by a cold, dry winter (May–September) (Mills 1990). Breeding occurred most frequently during the summer months (November–March) but, over the five years of the study, births were observed in all months of the year (Clutton-Brock *et al.* 1999*a*). For the purpose of these analyses, we defined the breeding season as the period between 1 September and 31 March.

All study groups were habituated to close observation by daily visits to the burrows. On average, 39 males and 34 females over six months old were monitored in each year of the study. All groups would tolerate observation from within 10 m and most group members could be weighed at regular intervals (Clutton-Brock *et al.* 1998). Most individuals could be recognized by scars or other idiosyncrasies, while around half were marked with metal ear-tags or transponders to aid identification. Animals reached adult weight (650 g) at around 15 months, although few bred before they were two years old. Mortality was high, with adults (individuals over one year old) having a life expectancy of less than one year (Clutton-Brock *et al.* 1999*a,b*).

Breeding data were collected during regular (often daily) visits to groups between February 1993 and April 1998. Pregnant animals could be identified from around the midpoint of gestation, which lasted for *ca.* 70 days (Clutton-Brock *et al.* 1999*a*). As parturition approached, pregnant females became evidently distended and it was immediately obvious when birth (or abortion) had occurred. For each breeding event, the date of birth, dominance status of the mother, litter size at emergence, and numbers of pups surviving to three months were recorded. Females were defined as breeding synchronously if they gave birth within ten days of each other: most attempts to breed by subordinates were synchronized with a breeding attempt by another group member, usually the dominant female. Breeding attempts by subordinates were classified as before those of the dominant female if they occurred when the dominant was visibly pregnant. After birth, pups remained below ground for approximately the first two weeks of life and then began to emerge at the burrow entrance. Litters were judged to have died if the breeding group left no babysitter at the breeding burrow on two successive days (see Clutton-Brock *et al.* 1998), or when the group changed burrow without taking the pups with them. At around 21 days, pups began to travel with the group, commonly changing sleeping burrows on successive nights (Clutton-Brock *et al.* 1999*a*).

The frequency with which animals left groups was monitored during regular visits to groups every one to four weeks. Where individuals of less than six months disappeared from groups, we assumed that they had died, for emigration was never observed in animals below this age. Animals over this age were only recorded as having left the group when they had been absent for at least 24 h and had been seen on their own or with another group. In some cases, more than one individual left the group at the same time (see below) so, to avoid inflating sample size, we treated multiple emigrations as single events. Our analyses used *G*-tests (applying Williams' continuity correction in analyses with one degree of freedom (d.f.)), Mann–Whitney *U*-tests for unrelated samples and Wilcoxon one-sample tests for related samples.

3. RESULTS

(a) *Infanticide*

Six cases of infanticide were observed directly. In all these cases, female group members carried pups out of a breeding burrow where they had been born less than 24 h earlier and killed and/or ate them in the presence of an observer. In two cases, the infanticidal animal was a pregnant, dominant female; in three cases, it was a pregnant subordinate female and in one case, a non-pregnant subordinate female. In all six cases, females killed the pups of close relatives: in two, females killed the offspring of their maternal sibs; in one case each, they killed the offspring of their mother, daughter, maternal cousin and maternal niece. Neither immigrant nor natal males were ever observed to kill pups in their own group. In addition, we observed four cases where pups were killed by members of neighbouring groups that temporarily invaded the territory of the breeding group and chased the babysitter away from a breeding burrow. Pups killed by neighbouring groups included pups of up to two weeks of age.

Indirect evidence indicates that dominant females commonly kill pups born to subordinates. Of 107 litters born to dominant females, 15% failed to produce emerging pups, whereas of 35 litters of pups born to subordinate females, 49% failed to produce emerging pups ($G=14.84$, d.f.$=1$, $p<0.001$). Litters born to subordinates most frequently died within 24 h of birth, the period when direct observation indicates that infanticide is most likely to occur. Median age at death for nine litters born to subordinates that failed to emerge was 1 day (interquartile range, 0–2 days), whereas the median age at death for nine litters born to dominants that failed to survive was 7 days (interquartile range, 1–11; Mann–Whitney *U*-test, $n=9,9$, $U=63.5$, $p=0.051$). For litters born to subordinates, the timing of their birth relative to the breeding status of the dominant female was closely related to this probability of survival. Of 11 litters born to subordinate mothers during the 70-day gestation period of the dominant female, none survived to emergence, whereas 59% of 22 litters born to subordinates during the 70 days after the birth of the dominant's pups (the approximate period when juveniles were dependant on other group members for food) produced pups that survived to emergence ($G=13.7$, d.f.$=1$, $p<0.001$). In contrast, for litters born to dominant females, there was no evidence that survival varied with the timing of birth relative to the breeding status of subordinates. Of 13 litters born to dominant females during the 70 days preceding a birth by a subordinate female in the same group, seven produced pups that survived to emergence, whereas of 12 litters born to dominants within 70 days after the birth of a litter to a subordinate female, ten produced surviving pups ($G=2.41$, d.f.$=1$, $p>0.1$).

There was no evidence to suggest that pups born to subordinates were less healthy than those born to dominants. Six litters born to subordinates had a median weight at emergence of 113.5 g (interquartile range, 87–130 g), compared with 34 litters born to dominant females, which had a median weight of 98 g (interquartile range, 84–113 g; Mann–Whitney *U*-test, $n=6,34$, $U=74$, $p=0.20$). Moreover, once pups had emerged, there was

no difference in survival to three months between pups born to subordinate and dominant mothers: mean survival from emergence to three months for six litters born to subordinates was $68.1 \pm 8.7\%$ compared with $69.8 \pm 3.6\%$ for 81 litters born to dominants.

(b) *Expulsion and emigration*

Dominant females frequently expelled subordinate females from the group during the latter months of their own pregnancy, but allowed them to return soon after birth. Subordinate females left their natal groups on a total of 31 occasions during the course of the study, although eight females left at the same time as one or more other individuals of the same sex, reducing the sample of independent emigrations to 27. Leaving was not confined to situations where the leaving female was closely related to the breeding adult of the opposite sex: of 17 females that left their natal group, the date of birth of which was known, 12 were neither sisters of the dominant male nor were conceived during his period of tenure. In 15 out of the 20 cases where one or more females left a group and the group was observed over the period of emigration, the breeding female was seen to chase and attack the prospective leaver repeatedly within three days of her emigration, and attacks could have occurred in the remaining five cases as groups were not visited every day. Attacks typically consisted of repeated chases, which sometimes involved other group members of both sexes as well as the dominant female. Attacks occurred in groups of all sizes, including two cases where the subject was the only female in the group apart from the dominant female. Ejected females typically followed the group for several days before leaving the area.

Most subordinate females were expelled during the last four weeks of the dominant female's 70-day pregnancy. Of 28 cases where one or more females left their natal group, 82.1% did so in the breeding season (September–March), compared with only 17.9% during the rest of the year ($G = 7.14$, d.f. $= 1$, $p < 0.01$). In total, 29 females were expelled during the dominant's pregnancy and 23 of these expulsions occurred during weeks 7–10, representing a highly significant increase in the frequency of females leaving groups during this period ($G = 18.39$, d.f. $= 1$, $p < 0.001$; see figure 1). This was not merely the product of correlated seasonal fluctuations in breeding and emigration, for the same pattern occurred when analysis was restricted to females leaving during the second breeding attempt of the season. Of seven females leaving their groups within ten weeks of the second conception by the dominant female of their group in the same year, six left between weeks 6 and 10 of the dominant female's pregnancy and the remaining animal did so in the fourth week, representing a higher rate of leaving between weeks 7–10 of the dominant female's second pregnancy compared with the previous six weeks ($G = 5.86$, d.f. $= 1$, $p < 0.05$).

Females that were expelled were usually over a year old: in all cases where females less than a year old left their groups, they did so at the same time as one or more older females. Of 25 females of known age that left their natal groups, six (24%) were over 36 months, six (24%) were between 24 and 36 months, eight (32%) were between 12 and 24 months, and five (20%) were between
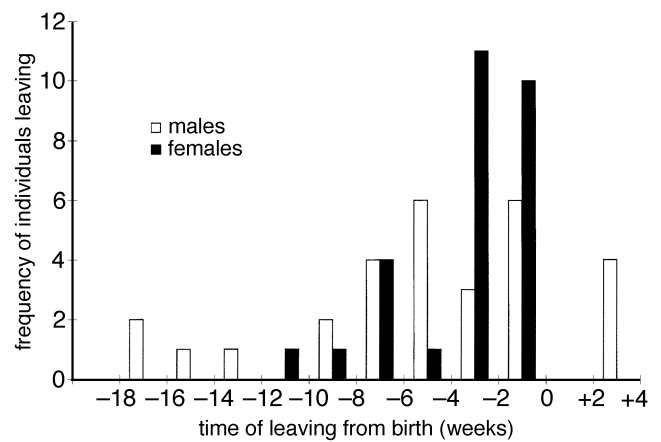

Figure 1. Frequency of females (filled bars) and males (open bars) leaving their groups ($n = 29$ and 28, respectively) in different weeks, relative to the timing of birth by the dominant female (birth $= 0$).

6 and 12 months. Only one out of the 15 females that were attacked and subsequently left the group was evidently pregnant and recent studies using a portable ultra-sound scanner confirm that many of the females that are expelled are not pregnant (P. N. M. Brotherton, unpublished data). Most females that were expelled were closely related to the breeding female: in six out of 14 attacks where the leaver's relationship to the dominant female was known, the recipient was the (maternal) sister of the dominant female; in three cases, she was the dominant female's daughter; and in five cases, she was either the dominant female's daughter or her niece. In nine out of the 15 cases where females were expelled from the group, one or more adult females remained in the group throughout the breeding attempt. These females were neither younger (Wilcoxon one-sample test, $W = 17$, $n = 9$, $p = 0.67$) nor lighter ($W = 28.5$, $n = 9$, $p = 0.515$) than females that left the group.

Of females that left their natal group, 57% subsequently returned to it (see table 1a), usually within the first four weeks after the dominant female gave birth (see table 1b). Females that returned spent, on average, 13.6 days ($n = 15$) away from their groups. Leavers that returned joined other group members in babysitting and subsequently feeding the dominant female's pups (Clutton-Brock *et al.* 1998).

Patterns of group leaving by males showed contrasts as well as similarities with females. Thirty-one males left their natal groups during the course of the study, although 11 males left at the same time as one or more other males, reducing the sample to 24 independent events. Of these, 83.3% occurred between September and March and 16.7% during the rest of the year ($G = 6.80$, d.f. $= 1$, $p < 0.01$). There was no significant difference in the age of males and females leaving groups (Mann–Whitney U-test, $Z = 1.81$, $n = 25$, 29, $p > 0.05$). Of 29 males of known age leaving their groups, 11 (37%) were between 6 and 12 months old, nine (31%) were between 12 and 24 months, four (14%) were between 24 and 36 months, and five (17%) were over 36 months old.

In contrast to females, male emigration was very rarely preceded by observed aggression directed at the emigrant by other group members of either sex. Of 16 emigration

Table 1. *Number of animals emigrating from, and returning to, their natal group*

(*a*) Number of animals that left their natal group (*n*) and that did not return or that rejoined the group within or after three months of leaving

| | number of animals leaving *n* | number of animals not returning | number of animals returning to natal group | |
			< 3 months after emigration	3–12 months after emigration
females	30	13	15	2
males	33	17	16	0
total	63	60	31	2

(*b*) Number of animals rejoining their natal group after leaving (*n*) that did so at different times relative to the parturition date of the dominant female

| | | number of animals returning to natal group within three months of leaving | | | |
	n	−2 weeks to birth	birth to +2 weeks	+2 to +4 weeks from birth	after 4 weeks from birth
females	15	3 (20%)	9 (60%)	1 (6.7%)	2 (13.3%)
males	16	4 (25%)	4 (37.5%)	0 (0%)	2 (12.5%)

events involving one or more males, emigration was preceded by observed chases in only one case, a significant difference from the situation observed in females ($G = 18.68$, d.f. = 1, $p < 0.001$). In addition, the timing of male emigration was less closely related to the breeding status of the dominant female than the timing of female emigration: whereas 76.6% ($n = 30$) of females that emigrated during the breeding season left during the last four weeks of the dominant female's pregnancy, only 31% ($n = 29$) of departing males did so ($G = 12.52$, d.f. = 1, $p < 0.01$).

4. DISCUSSION

Infanticide by resident females is common in suricates, as in many other mammals (Sherman 1981; Hoogland 1994; Rasa 1994; Doolan & Macdonald 1997). Five out of the six cases of observed infanticide involved pregnant female relatives killing pups less than 24 h old: males and lactating females were not observed to kill pups born in their own group, and a female that was not evidently pregnant was only observed to do so on one occasion. Circumstantial evidence suggests that pregnant, dominant females frequently killed pups born to subordinate females.

Breeding females probably benefit from infanticidal behaviour as the amount of food received by pups from other group members declines as the pup : helper ratio increases (T. H. Clutton-Brock *et al.*, unpublished data). By ensuring that there are no older (and consequently larger) pups in the group at the same time as her own, mothers ensure that their pups have an advantage in competition for food.

By expelling subordinate females from the group during the later stages of gestation, breeding females presumably reduced the risk of infanticide. Expulsion may have been the only feasible strategy, for dominant females spent little time at the breeding burrow during the first three weeks after their pups were born (Clutton-

Brock *et al.* 1998) and, consequently, it would not have been possible for them to have ensured that particular group members did not gain access to the pups. Although the removal of adult females from the group probably improved the survival chances of the dominant female's pups during the neonatal period, expelling subordinates had appreciable costs as the presence of additional helpers reduced the workload of breeders and survival increased with group size (Clutton-Brock *et al.* 1998, 1999*b*). It was presumably for this reason that dominant females frequently allowed subordinate females to return once they had given birth. No females that were allowed to return to the group by the breeding female after she had given birth subsequently attacked her pups or gave birth to a litter of their own within 70 days of returning to the group. Consequently, the costs of allowing subordinate females to return to the group once pups had been born were probably low.

Subordinate females rarely, if ever, left groups of their own volition. The survival of adults increased with group size, suggesting that they gained direct benefits by remaining in their group (Clutton-Brock *et al.* 1999*b*). In addition, subordinate females probably increased their chances of attaining the dominant position by remaining in their natal group: of 12 dominant females that we have followed, seven acquired the dominant role by remaining in their natal group, five did so by forming new groups with males that had emigrated from other groups, and none immigrated into established groups. Evidence that subordinate, non-breeding females attempted to remain in their natal group suggests that it is unlikely that successful breeding attempts by subordinates were the result of concessions granted by dominants with the objective of retaining them in the group (see Keller & Reeve 1994).

Unlike females, males were never observed to kill pups in the group to which they belonged and, where males left groups, they usually did so of their own volition. Emigration probably represented a more attractive option to

subordinate males than females because emigrant males were allowed to join established groups and seldom acquired the breeding position in their natal group. Out of 19 dominant males that we monitored, only two had been born in the group that they bred in, five were founding members of a group, and 12 had immigrated into the group that they eventually bred in as adults. Males, like females, commonly left their natal packs when the dominant female in the pack was pregnant (figure 1). There may have been at least two benefits to males of leaving at this time. First, as breeding was broadly synchronized across groups, dispersing males commonly located groups of females that had been expelled from their group and formed new groups. Second, by leaving before the dominant female gave birth, males avoided becoming involved in costly cooperative behaviour during the imminent breeding attempt (see Clutton-Brock *et al*. 1998).

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