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SHORT COMMUNICATION

Kidnapping and infanticide between groups of banded mongooses

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In social mammals, group size is a crucial determinant of success (Courchamp et al. 1999). Individuals in small groups are not only more susceptible to predation (Krebs and Davies 1993) but also less successful in rearing young (Jennions and Macdonald 1994; Clutton-Brock et al. 1999). Neighbouring groups also frequently compete intensely for resources (Schaller 1972; Goodall 1986; Mech and Boitani 2003) and smaller groups are usually inferior in antagonistic encounters with neighbours (Grinnell et al. 1995; Cant et al. 2002). Therefore, group-living animals benefit from increased group sizes both absolutely and relative to their neighbours (group augmentation; Woolfenden 1975; Kokko et al. 2001).

It is not surprising, therefore, that many mammals are aggressive and frequently infanticidal towards the offspring of neighbours (Ebensperger 1998; van Schaik 2000), presumably to eliminate competitors for themselves or their offspring. In contrast, kidnapping between social units is rare (Mohnot 1980; Nakagawa 1995) and its occurrence is hard to explain since the costs of raising foreign offspring are expected to select against it. In certain cases however, particularly in cooperatively breeding species, these costs may be outweighed by the benefits of an increased group size (Heinsohn 1991). Therefore, kidnapping may sometimes be adaptive rather than a by-product of parental behaviour and associated hormonal changes as has been suggested for primates and penguins (Itani 1959; Jouventin et al. 1995). Crucially, aggressive and alloparental behaviour towards foreign offspring are not mutually exclusive but may be conditional strategies within the same species.

Here we report observations of inter-group infanticide and kidnapping in a population of banded mongooses (*Mungos mungo*) in Queen Elizabeth National Park, Uganda. Banded mongooses are small (<2 kg) carnivores and live in social groups of 5–60 individuals. Within groups, several females commonly give birth synchronously and the group cares cooperatively for the litter (Cant 2000). Non-breeding helpers contribute to pup care by babysitting the litter (first 3 weeks after birth of the litter; Cant 2003) and later by provisioning the offspring until they are independent (at an age of about 3 months; Gilchrist 2004; Hodge 2005). Between May 2003 and October 2005, we regularly visited 10 habituated groups, on average seven times per week (0–2 times per day). During this period, we observed two kidnapping events and 12 cases of infanticide between groups.

The kidnapping events involved a small group of seven adult females (group 1N), which had recently been evicted from their natal group, and a large group consisting of 14 adult males, 6 adult females and various infants and pups (group 1B; Fig. 1). The first kidnapping event occurred on 31 August 2004. The females of group 1N, none of which were pregnant or lactating at

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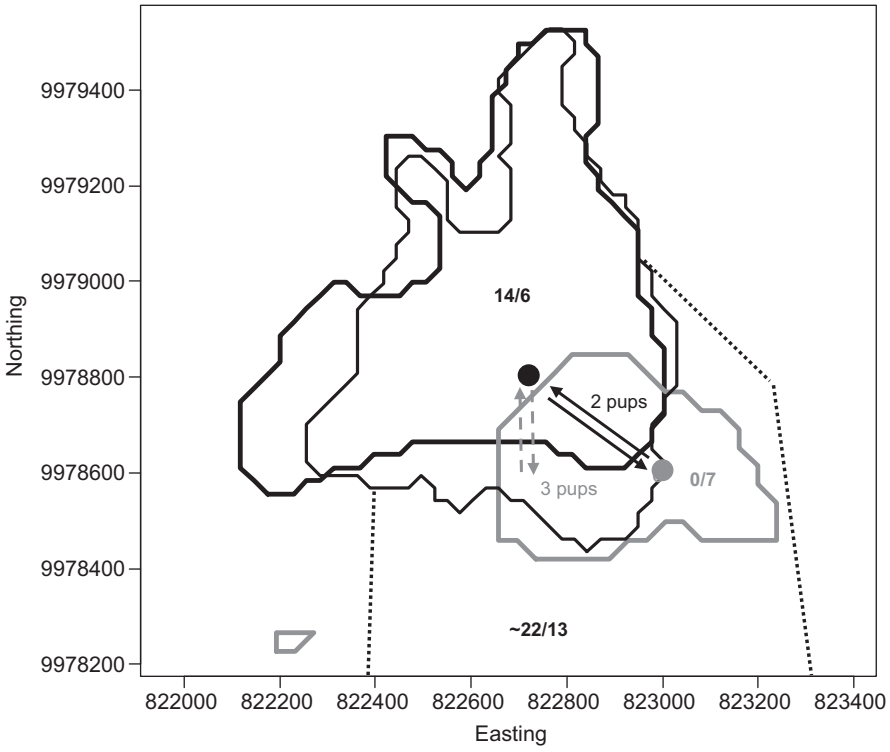

Fig. 1. Home ranges of the two groups involved in the kidnapping events (black: 1B, grey: 1N). For group 1B, home ranges in 2004 (thin line) and 2005 (thick line) are given separately. Home range contours were calculated as 90% Epanechnikov kernels (Epanechnikov 1969) using the adehabitat package for R (Calenge 2006). Dashed lines sketch part of the home range of a large neighbouring group (group 2). Group sizes as of September 2004 are given as number of adult males/number of adult females. Den sites from which pups were kidnapped are marked with filled circles. Dashed arrows: first kidnapping event (31 August 2004). Solid arrows: second kidnapping event (29 October 04).

the time, found the den of group 1B, in which a litter born 10 days previously had been left temporarily unattended by babysitters. Group 1N removed three pups from the den and left at least three more pups behind. The kidnappers carried the pups with them for 2 days, during which they were repeatedly observed suckling the pups. In three females allolactation was confirmed by gentle stimulation of the teats. On 2 September, group 1B encountered group 1N and retrieved the kidnapped pups. No pup of this litter, either kidnapped or left at the den, survived to independence, probably due to poor environmental conditions (July/August 2004 was the driest 2-month period during the whole study).

The second kidnapping event occurred on 29 October 2004 and involved the same two groups but with reversed roles. Five of the seven females in group 1N had given birth 3–4 days previously. Three of the six females of group 1B were in the latest stages of pregnancy, but none of them had given birth yet. Three adult males from group 1B had joined group 1N temporarily during their post-partum oestrus. These three males then removed at least two pups from the group 1N den and carried them to their own group's den, about 300 m away. It is not known how long these two pups survived thereafter. The females of group 1B gave birth in the same den over the following 3 days and their litter emerged for the first time on 11 November. We cannot exclude that the kidnapped pups were killed on the day of kidnapping by group members other than the kidnappers, nor can we exclude that they survived and emerged with the 1B litter.

During the same study period, we recorded 12 occasions when pups were killed by neighbouring groups (Table 1). The killings were observed directly or dead pups were recovered after fights between groups (six events), or pups were present and healthy before a fight but missing the day after (six events). In total, 17 pups (age 22–94 days) from five groups were killed or presumed killed by six different groups. With one exception, killed pups belonged to the smaller of the two groups engaged in an aggressive contest and the largest group in the study area was responsible for 50% of the observed infanticide events between groups. On several other occasions, groups found the den where neighbouring groups were babysitting pups less than 3 weeks old. On these occasions, we were unable to determine whether pups were killed since no bodies were

Table 1. Infanticide events between banded mongoose groups

Date	Affected group[a]	Number of pups killed	Age of pups (days)	Aggressor group[a]	Note[b]
14/08/03	12 (6)	1	31	1B (20)	Observed
01/10/03	1K (10)	2	26	1C (10)	Assumed killed
17/01/04	11 (14)	1	94	2 (>30)	Observed
11/07/04	1K (10)	2	40	1B (26)	Observed
01/03/05	1H (20)	1	27	11 (16)	Assumed killed
25/04/05	1N (5)	1	22	2 (>40)	Observed
25/04/05	1N (5)	2	26	2 (>40)	Assumed killed
30/04/05	1N (5)	1	27	2 (>40)	Observed
14/05/05	12 (6)	1	33	1H (23)	Assumed killed
24/05/05	1N (5)	2	51	2 (>40)	Assumed killed
25/05/05	12 (6)	1	44	1B (26)	Assumed killed
20/07/05	1B (26)	2	28/37	2 (>40)	Observed

[a]Group size (number of adults) is given in brackets.
[b]Observed: killing was observed directly or bodies were found after a fight; assumed killed: pups were present and healthy before but missing after a fight.

recovered and an accurate count of the litter was not possible until later. However, J.S. Gilchrist (unpublished data) on two occasions observed an adult entering the den of a rival group, dragging a pup out and killing it.

A variety of hypotheses have been proposed to explain kidnapping behaviour, most of which are highly unlikely to apply in the present cases. Kidnapping may be a non-adaptive by-product of parental behaviour and increased hormone levels associated with it. This may explain the behaviour of primates (Itani 1959) and penguins (Jouventin et al. 1995; Angelier et al. 2006) which have recently lost their own offspring and then kidnap foreign offspring. It is unlikely to apply here since the kidnappers were either males or non-breeding females that had not been pregnant for 4–5 weeks prior to the event and neither of the two 'kidnapper groups' had pups themselves at the time nor had they lost a litter recently. For the same reason it is unlikely that foreign pups were considered as own pups (i.e. recognition errors; Bustamante and Hiraldo 1990). However, for the second event we cannot rule out the possibility that the kidnapping males were hormonally primed to provide care as is observed in male tamarins shortly before their females give birth (Ziegler et al. 2004). Finally, Lancaster (1971) suggested that kidnappings serve as an opportunity to gain experience with handling offspring. Again, this is unlikely to apply here since the three kidnapper males had previously contributed to rearing several litters in their own group and six of the seven kidnapper females had given birth to several litters previously while still in their natal group.

We suggest that kidnapping in the banded mongoose is an adaptive, if rarely occurring behaviour with the goal of group augmentation (*sensu* Kokko et al. 2001). In banded mongooses, small groups are at a disadvantage in competition with neighbouring groups (Cant et al. 2002) and they have little success in rearing young (Cant 2000; Gilchrist 2006). Similar to white-winged choughs (Heinsohn 1991), recruiting individuals which have already survived a part of their most vulnerable life stage without bearing the costs of pregnancy may be a reasonable strategy for groups that are small in absolute numbers (like group 1N) or are small in relation to their neighbours (like group 1B). Indeed, group 1N only managed to rear pups themselves at their third attempt, in April 2005 and group 1B lost a valuable part of their territory, including preferred den sites and reliable food sources, to the larger neighbouring group 2 during the study period (Fig. 1). Also, for both kidnapping groups the litter before the event had failed and the two groups were closely related which may have promoted kidnapping in these cases. However, kinship alone is unlikely to promote kidnapping since seven of the ten study groups are connected by dispersal links and infanticide is nevertheless the predominant behaviour towards foreign pups.

To conclude, our detailed observation of the two kidnapping events indicates that several present hypotheses that attempt to explain this behaviour are unlikely to apply here. Instead, we suggest that kidnapping and infanticide of pups from neighbouring groups may both be strategies to increase the group size relative to the neighbours and are used conditionally in the banded mongoose. This notion is further supported by the finding that both groups involved in the two kidnapping events have also killed foreign pups on other occasions (group 1B: Table 1; group 1N: N.R. Jordan, personal communication). Whereas infanticide occurs commonly in the banded mongoose, kidnapping may only be used under restricted circumstances and may only be possible when unattended pups are encountered, as babysitters may prevent kidnapping more effectively

than infanticide which requires access to the pup for only a few seconds (M.B.V. Bell and C.A. Müller, personal observation).

Reports of kidnapping between social units, including the present one, usually present small sample sizes. However, the apparent rarity of this behaviour makes these anecdotal reports nevertheless valuable. We suspect that kidnapping may be an adaptive behaviour in other cooperatively breeding species and we encourage reports since these will, accumulated over time, shed light on the adaptive or non-adaptive causes of this puzzling behaviour.

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