

Fighting and Mating Between Groups in a Cooperatively Breeding Mammal, the Banded Mongoose

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Abstract

Many cooperatively breeding animals actively defend a territory containing resources such as food and shelter, which are essential for reproduction. Some observations, however, indicate that conflicts between groups are often triggered by the attempts of males or females, or both, to gain extra-group copulations. We studied interactions between 12 groups of banded mongooses (*Mungos mungo*) in Uganda to test whether the frequency of inter-group encounters was linked to the reproductive status of females, and conducted an experiment to examine the responses of individuals to mongooses from other groups. The rate at which focal groups fought with other groups was higher when its females were in estrous, suggesting that many fights take place over access to mates. Both males and estrous females were instrumental in instigating encounters with rival groups, and extra-group copulation in the midst of a fight was observed on three occasions. We experimentally simulated encounters with foreign individuals by presenting each of six groups with cages containing a male and a female from a rival group. Subordinate males were the first to investigate these 'intruders', spent more time around the intruders' cages, and were more aggressive to the intruders than either dominant males or females. Subordinate males directed more attention and aggression towards the male intruder than the female intruder. We suggest that male banded mongooses actively seek extra-group copulations in pursuit of paternity, while females may actively seek extra-group copulations as a way of reducing inbreeding depression.

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Introduction

Many animals that live in cooperatively breeding groups actively defend their territories from conspecific rivals (Brown 1987). A considerable amount of

theoretical work has been directed towards understanding the evolution of territoriality in animals in general (Dill 1978; Parker & Knowlton 1980; Davies & Houston 1984), and social animals in particular (Brown 1982; Bacon et al. 1991). Group territoriality is expected to evolve where the benefits of joint defense of the resources in a territory outweigh the costs of sharing those resources with other group members (Brown 1982; Davies & Houston 1984). The resources in question will usually be in the form of food (see examples in Stacey & Koenig 1990), but may also comprise topographical features (e.g. dens, bushes, rocks) which provide protection from predators (Rood 1986; Balshine-Earn et al. 1998). Because possession of a suitable territory is a prerequisite for reproductive success in most cooperatively breeding birds and mammals, territorial defense may often be the most important cooperative activity in the group (Heinsohn 1997).

The burden of defending the territory often falls unequally on group members. In particular, males commonly put greater effort into territorial defense than do females (Ridpath 1972; Kinnaird & Grant 1982; Craig 1984; Petrie 1984; Gwinner et al. 1994; Grinnell et al. 1995). Moreover, males of several species direct most of their aggression towards other males (Gwinner et al. 1994; Baker & Dietz 1996; Levin 1996), suggesting that many 'territorial' disputes may actually represent conflict over access to mates (Putland & Goldizen 1998; Steenbeek 1999). For males, extra-group copulations (EGCs) are likely to bring clear rewards in terms of direct fitness (Birkhead & Møller 1992). For females, the advantages of EGCs are less clear, but the fact that they sometimes actively seek EGCs suggests that females too can gain substantial benefits from mating outside their social unit (Gagneux et al. 1997; Wrangham 1997).

In the current study we investigated the frequency and timing of encounters between neighboring groups of free-ranging banded mongooses (*Mungos mungo*) and recorded the behavior of males and females during these encounters. We also experimentally investigated the behavioral responses of males and females, dominants and subordinates to 'intruders' from foreign packs. Banded mongooses are small, diurnal herpestids that live in cooperative groups averaging 18 individuals. In Queen Elizabeth National Park, Uganda, these groups reproduce three to four times a year (Rood 1974, 1975, 1986; Cant 2000; Cant et al. 2001; De Luca & Ginsberg 2001). Groups or 'packs' occupy home ranges containing numerous communal dens, between which packs typically move every 2 or 3 days (Cant 1998). Reproduction is synchronized within but not between packs (Rood 1975), with the period for which female packmates are in estrous lasting for an average of 6 d (Cant 2000). Encounters between neighboring packs are common and involve intense aggression. In a pioneering study, Rood (1975) observed 15 aggressive encounters between packs of banded mongooses, and reported that in the middle of these fights mating sometimes occurred between the males and females of opposing sides. It is not known, however, whether these matings are opportunistic or whether males or females actively seek extra-group matings.

Methods

Animals and Study Site

We studied a population of 341 mongooses living in a total of 14 packs on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 27°54'E) between Nov. 1995 and Aug. 1997. Mweya Peninsula is a 5-km² heart-shaped promontory extending into Lake Edward, connected to the mainland by a narrow ridge. The habitat is medium-height grassland, scattered with *Euphorbia candelabrum* trees and thickets of *Capparis tormentosa*. Annual rainfall is typically 800–900 mm. Further details of the study area are given elsewhere (Rood 1975; Cant 1998, 2000; Cant et al. 2001; De Luca & Ginsberg 2001).

The density of banded mongooses at the Mweya site is very high. For example, in Aug. 1996, their density on the peninsula was 28 individuals/km² (Cant 1998). By comparison, banded mongooses in the Serengeti in Tanzania live at a density of 1.8 individuals/km² (Waser et al. 1995). At the Mweya site, packs averaged 18 individuals (> 6 mos old), plus an average of 2 pups/infants under 6 mo of age. The home range area of nine Mweya packs averaged (\pm SE) 68.5 \pm 7.1 hectares. For a map of the study area including home ranges, see Cant et al. (2001).

We captured mongooses using baited live traps (67 \times 23 \times 23 cm; Tomahawk Co. Wisconsin) and anaesthetized them using a combination of 1.4 mg ketamine (Vetalar: Veterinary Drug Company (VDC)) and 1.2 mg medetomidine (Domitor: VDC) injected into the femoral muscle. Smaller animals received 67% of these doses; animals under 3 mos old were not anaesthetized. Adults were measured, weighed, and fitted with color coded plastic collars which enabled individuals to be identified. We marked sub-adults and infants by shaving a small (c. 4 cm²) area of fur from the rump. One or two adult animals in each pack were fitted with a radiocollar (Telonics Ltd, Mesa, Arizona) with a 20-cm whip antenna. After handling, mongooses were injected with 1.2 mg atipamezole preparation (Antisedan: VDC) to reverse the effects of medetomidine, and placed in a covered bucket for 1–2 h to recover. When fully awake, the animals were released at the trapping site. No animals died or became sick as a result of the trapping procedure.

Encounters Between Free-Ranging Groups

We located packs using radiotelemetry and approached on foot until the animals were sighted. Packs were usually followed on foot by one or two observers for a whole morning (07:30–12:00 h) or afternoon (15:30–19:00 h) foraging session. We defined an 'encounter' as an occasion where two packs sighted each other. This was readily ascertained because of the conspicuous reactions of the mongooses (described below), and because all encounters led to a confrontation of some sort. Detailed observations of the encounters were spoken into a dictaphone or written down. We recorded the identity of both packs, their location, and, where possible, the duration of the encounter and its outcome. Some encounters,

however, took place in areas of thick vegetation, in which case it was not possible to determine the duration or outcome of the encounters with accuracy.

To measure the frequency with which a particular pack was involved in encounters or fights, we counted only those occasions that a pack encountered another while it was being followed (i.e. when it was the 'focal pack'). The opposing 'rival' pack was not scored as having had an encounter unless a second observer was also following it at the time. This enabled us to test whether packs were more likely to be involved in fights at certain times (for example when the females were in estrous) than others, without introducing a systematic sampling error. The encounter rate for each pack was then calculated as the number of encounters while being followed divided by the number of hours for which the pack was followed.

Home ranges were estimated by plotting the location of packs and their dens on an aerial photograph of the study area, divided into 1-hectare squares. The borders of these home ranges were often defined by natural features (e.g. the lake shore, erosion gullies) and by shared marking posts (large stones, branches, etc.) at which members of adjacent packs anal marked, chin marked or deposited feces at each visit. Home ranges were plotted by drawing straight lines between the most peripheral dens or marking posts used during the study, yielding a minimum convex polygon whose area was then calculated. There was considerable overlap between the home ranges of neighboring groups: on average, about 27% (range 10–55%) of a group's home range overlapped with the that of one or more neighboring packs.

Most encounters took place when packs came across each other in areas of overlap between their respective home ranges. However, when one of the packs included estrous females, encounters sometimes took place deep within the home range of one or the other pack. Encounters were categorized according to their location and the reproductive state of females as follows: (i) incidental encounters, encounters which occurred in the area of overlap of two packs' home ranges, at a time when neither pack contained estrous females; (ii) female forays, encounters which resulted from estrous females leading their group outside the area of overlap between neighboring packs into the exclusive home range of a neighbouring pack; (iii) male forays, encounters which occurred when males led the group outside the area of overlap between neighboring packs into the exclusive home range of a neighboring pack, whose females were in estrous. Although rare, 'forays' were conspicuous behavioral events and it was easy to recognize which individuals led them because they moved ahead of the rest of the group whilst calling frequently. These three definitions cover all observed encounters, because non-estrous females never led forays into the ranges of neighboring groups, and males never forayed into the ranges of groups whose females were not in estrous.

Simulated Encounters with Caged 'Intruders'

The behavior of individuals during natural encounters was difficult to quantify accurately because of the number of animals involved, the speed at which

individuals chased each other, and the thickness of the vegetation. To examine the responses of individual group members in more detail, we staged encounters with caged individuals from a neighboring group. First we washed two live traps in soap and water to minimize any residue scents from previous trapping sessions, and then used these traps to capture an adult male and an adult female from the same group. For the purposes of the experiment, these two individuals were named 'intruders' and the group from which they came was denoted the 'foreign pack'. Trapped animals were covered with a cloth (to minimize stress) and transported by car to the home range of a neighboring pack ('the resident pack'). Both intruders (still in their traps) were placed 5 m apart in the foraging path of the resident pack and uncovered. Observers with binoculars sat 20 m away. The experiment was timed from the moment the resident pack responded to the traps, and continued for a maximum of 10 min, or until the resident pack moved on. We recorded the response of the resident pack and the identity of the first individual to approach one of the traps. At 30-s intervals we scored the number and, where possible, the identity of individuals located within 0.5 m of each trap. There were sometimes too many individuals around the traps to record the identity of each, but on almost all intervals we were able to record their sex and age class.

We recorded ad libitum acts of aggression by members of the resident pack. Distinctive 'snaps' (mock or attempted bites, often accompanied by a short bark) and pounces at the cage were scored as aggressive acts. The response of the intruders varied from apparent disinterest to aggressive snapping, but it was not possible to score these reactions accurately because the intruders were frequently obscured from view by members of the resident pack. At the end of the trials, we covered the intruders' traps with cloth and returned them to their own group for release. As a matched control we used the same procedure but instead of using intruders from a foreign pack we captured a male and a female from a group, kept them covered in shade for 30 min, and then placed them in the foraging path of their own pack. Fourteen such trials were conducted on six packs between Aug. 1996 and July 1997. One control trial was performed on each of these six packs during Apr. and May 1997. On no occasion did we perform experimental or control trials on resident packs in which females were in estrous, nor were estrous females ever used as intruders.

We categorized males of the resident pack as 'dominant' or 'subordinate' depending on whether they had mate-guarded females in the most recent breeding attempt (Cant 2000). 'Breeding females' were those that had been pregnant in the last 6 mos. Females were categorized as 'subordinate' if they were over 6 mos old but had not yet been pregnant. We calculated an 'intruder inspection rate' for each dominance/sex category as follows. An individual that was less than 0.5 m from the trap at the start of an interval scored an 'inspection mark'. The total number of inspection marks by individuals of a particular dominance/sex category was divided by the number of intervals in the trials (20 if the experiment ran for 10 min, less if the resident pack moved on before then). This figure was then divided by the number of individuals of each category in the focal pack to obtain a per capita intruder inspection rate for each dominance/sex category.

Data Analysis

Non-parametric statistics followed the methods of Siegel & Castellan (1988) and were performed using the Statview 4.02 package. For the analysis of data from the intruder experiment, we used generalized linear modelling (GLM) in the GLMStat 4.0.3 program (© K. J. Beath; kjbeath@kagi.com) following the methods of Crawley (1993). Normal or Poisson errors were used as appropriate. Terms were subtracted from the model until further removals led to significant ($p < 0.05$) increases in deviance, as assessed from tabulated values of F or χ^2 . We report significance levels for terms when adding them last to this minimal adequate model.

Results

Natural Encounters

A total of 95 encounters were recorded between May 1996 and Aug. 1997. On 24 of these occasions, two packs were discovered together without either of them having been followed. The remaining 71 encounters involved 'focal' packs. Thirty-seven of these 71 encounters were between established packs with stable, contiguous home ranges. The remaining 34 encounters involved newly formed packs which were in the process of dispersing or were attempting to establish a home range. It was not possible to determine 'winners' and 'losers' for 48 encounters: normally this was because the fights took place in thick vegetation, which made observations impossible. In 47 out of the 95 encounters, however, one pack withdrew or fled and the other pack emerged as a clear winner. In 45 (96%) of these cases, the winner was the larger of the two packs (G-test: $G_1 = 48.6$, $p < 0.001$).

Behavior during encounters

Only one previous study (Rood 1975) has described encounters between groups in any detail. Rood observed 18 encounters, 15 of which led to direct fighting. In the other three cases the smaller pack withdrew before physical contact occurred. We augment Rood's account with the following descriptions of behavior during 'incidental encounters' and 'forays'.

Incidental encounters were initiated when two packs sighted each other. Members of both packs responded by standing erect and giving a distinctive, screeching call (which we named 'intruder' calls). These calls alerted the rest of their pack to the presence of a rival group. All 95 encounters involved aggression on the part of one or both groups. The sight of a large rival pack was sometimes sufficient to cause a small group of mongooses to flee, with members of the larger group chasing behind. Groups that were more closely matched in size bunched together and approached each other with more caution, stopping frequently to stand upright and stare at their opponents. Typically, members of the two groups approached to within 20–30 m of each other before rushing forward, with members of both packs fanning out and engaging in one-to-one fights or chases

with their opponents. Face-to-face confrontations between individuals were brief (< 5 s) and violent, involving repeated bites and scratches with the front paws until one of the combatants retreated. Packs that had become scattered sometimes retreated, bunched together, and advanced again. In this way, fights between large, evenly matched packs sometimes lasted for over an hour (see also Rood 1975), although it was more common for one pack to withdraw after 10–20 min of sporadic fighting.

Mongoose were seen bleeding and/or limping after being involved in a fight on a number of occasions, and on at least three occasions it was suspected that mongooses died from injuries sustained in these fights (for details see Cant et al. 2001). In one instance, we watched as a sub-adult male was cornered and repeatedly attacked by 10 adults from a rival group, after which he was seen limping and bleeding heavily from the mouth and rump. This male subsequently disappeared.

Observations of behavior during four male 'forays' suggested that olfactory cues provide information about the proximity of a neighboring pack. Each of the forays was initiated after a pack visited a marking site (e.g. a large stone) that was also used by a neighboring pack. After sniffing the marking site, the mongooses gave a twittering call and engaged in intense marking of each other and the site. This was followed by the males in the pack moving rapidly and directly into the neighboring pack's home range, stopping briefly to sniff at some points along the way. Females and pups followed towards the rear of the group. Focal packs traveled well outside their normal home range during these forays, once covering 500 m in less than 10 min. On three out of the four occasions, the foray culminated in direct confrontation with the resident pack.

Encounter rate and female reproductive status

Focal packs encountered other packs more frequently when females in the focal pack were in estrous than when they were not (median encounter rate: estrous = 0.059 encounters/h, non-estrous = 0.016 encounters/h; Wilcoxon signed rank test: $n = 12$ packs, $T^+ = 77$, $p < 0.05$). Encounters were more likely to occur outside of the normal area of overlap of home ranges if one of the packs contained estrous females (number of encounters outside home range when females of one pack were in estrous: 13 encounters out of 37; number of encounters outside home range when packs did not contain estrous females: 5 out of 58; binomial test: $n = 18$, $z = 2.66$, $p < 0.01$). Twenty-four (65%) of the 37 encounters involving a pack with estrous females occurred in the area of overlap between two packs' home ranges; nine (24%) were forays led by males, four (11%) were forays led by estrous females.

Extra-group copulations

We observed mating between members of different packs on three occasions. The first occurred during an 'incidental encounter'. Two packs, one of which

comprised 25 individuals (> 6 mos old), the other 14 individuals, met in an area of overlap between their home ranges. The males of the smaller group were attacked and driven off, but the two females in the smaller pack did not flee, and were not attacked. Instead, both females allowed males to mount them, and one female was seen to mate for 4 min. After the encounter both females returned to their own pack. Both these females had come into estrous and mated 3 wks prior to the extra-group copulation, yet both females came into estrous again within a few days of the encounter. This was one of only two occasions throughout the study where female banded mongooses were observed to re-enter estrous prior to parturition.

Two more EGCs were seen during a male foray into the home range of a pack of 24 individuals that contained estrous females. A dominant male and female were copulating when a number of males from a neighboring pack appeared, approximately 300 m outside the limits of their normal home range. A male from the neighboring pack, comprising 26 members, attacked and drove off the copulating male before mounting the female. The female remained where she was and accepted the intruder male's attempt to mate. At the same time, another female from the resident pack mated with one of the intruding males. After the mating both females returned to the den in which the pack had spent the previous night, where the rest of the pack had retreated.

Finally, an extra-group copulation occurred during a female-led foray by a group of 24 members into the home range of a neighboring pack of 25 members. A fight ensued, during which the female who had led the foray, and who was in estrous that day, was seen mating with a male of the resident pack. It was not known whether the male with whom she mated was dominant or subordinate within his own group.

On three other occasions, we suspected that extra-group copulation had occurred when estrous females were observed running off into or behind a thicket with a male from a rival pack following close behind, sniffing her genital area in the manner that normally precedes an attempt to copulate. In each case this happened in the middle of a fight between two packs, and in the confusion we were unable to keep track of the pair or watch them emerge from the thicket, which may have yielded indications as to whether mating had occurred (for example, both male and female banded mongooses usually lick their genital area after copulation). In Rood's (1975) study, extra-group copulation or attempted mounting was observed in two out of 18 encounters. In both cases females in one of the groups were in estrous at the time of the encounter.

Staged Encounters

Across six packs, the rate at which pack members inspected foreign intruders was over six times greater than the rate at which they inspected 'control' intruders (foreign intruders: median inspection rate = 0.08 inspections/interval/individual; controls = 0.012 inspections/interval/individual; Wilcoxon signed rank test: $n = 6$ packs, $T^+ = 21$, $p < 0.05$). It appeared that the mongooses could

recognize foreign intruders visually, from a distance of 10 m or more. Typically, one individual spotted the traps, stood upright, and gave an intruder call. Other members of the pack would also stand up, bunch together and then slowly advance towards the traps. The response to control intruders was very different: individuals approached the traps in a 'relaxed' manner and no intruder-call was given.

Subordinate males were more likely than other dominance/sex categories to be the first to inspect foreign intruders (G-test: sub-males vs. others; $G_1 = 5.398$, $p < 0.05$). In a generalized linear model, the dominance/sex categories of individuals had a significant effect on the rate at which they inspected intruders (GLM: $F_{3,52} = 5.3$, $p < 0.01$). All other terms in the model (resident pack identity, foreign individual's pack identity, resident group size) had no significant effect and were thus removed. Subordinate males inspected intruders at a significantly greater rate than other dominance/sex categories (Fig. 1). This reflects the difference in the manner in which different dominance/sex categories responded to the intruders. Usually the females of the pack stayed well back from the intruders while subordinate males moved forward to inspect the traps. Dominant males stayed close by the females, and only rarely came forward to inspect the intruders. Subordinate males inspected male intruders at a significantly higher rate than female intruders (Wilcoxon signed rank test: $n = 14$, $T^+ = 85$, $p < 0.05$; Fig. 1). The other dominance/sex categories exhibited no significant difference in the rate at which they inspected male and female intruders (Wilcoxon test, all $p > 0.05$). It is not known to what extent the behavior of the intruder influenced the rate at which they were inspected.

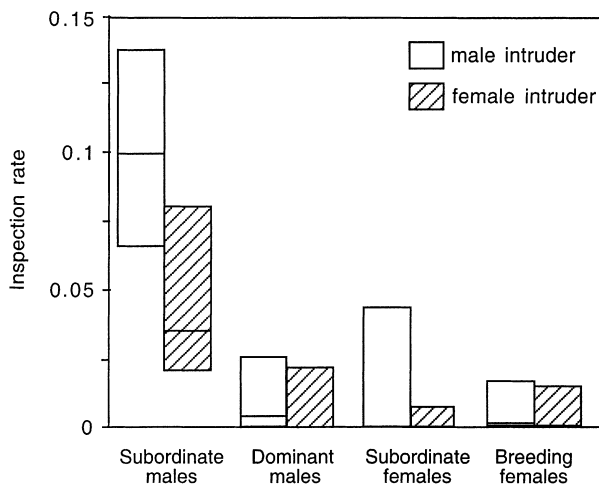


Fig. 1: Inspection rates of different sex/dominance categories towards caged male and female intruders. Inspection rates are expressed as the number of inspection marks observed per 30 s per category member. Data are from 14 trials of the experiment. Boxes show medians and interquartile ranges

A median of 0.105 (IQR = 0.168) aggressive acts per resident pack member was directed towards foreign intruders, whereas no aggressive acts at all were recorded in the control trials (Wilcoxon signed rank test: $n = 6$ packs; $T^+ = 21$, $p < 0.05$). Subordinate males were more frequently aggressive towards foreign intruders than dominant males, whereas breeding females and sub-adult females were never aggressive (GLM: $F_{3,52} = 4.8$, $p < 0.01$; Fig. 2). The identity of the resident pack, the intruders' pack, and the resident pack's group size had no significant effects on the rate of aggression and these terms were thus excluded from the model. Subordinate males directed significantly more attacks towards the male compared to the female intruder (Wilcoxon signed rank: $n = 14$, $T^+ = 84$, $p < 0.05$), Dominant males also attacked male intruders more frequently than females, but this difference was not significant (Wilcoxon signed rank: $n = 14$, $T^+ = 52$, $p < 0.1$). Again, it was not known whether the intruder's behavior influenced the amount of aggression directed towards it, but anecdotal observations suggest that male intruders tended to be more aggressive towards inspecting individuals than female intruders.

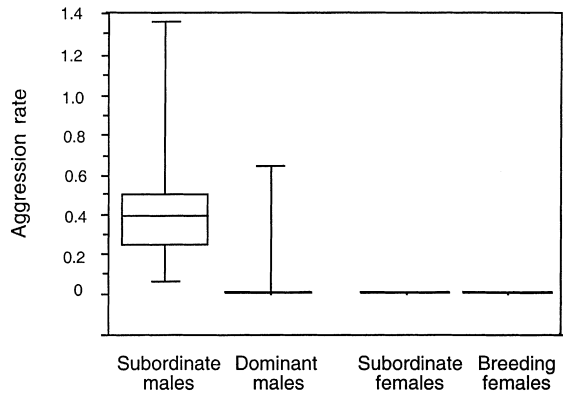


Fig. 2: Rates at which different dominance/sex categories were aggressive towards intruders in 14 trials of the experiment. Aggression rates are expressed as the number of aggressive acts observed per 30 s per category member. Boxes show medians and interquartile ranges, extending lines show 10th and 90th percentiles

Discussion

Relations between banded mongooses packs are highly antagonistic. Meetings between packs led to aggressive chases and fighting between both males and females, and individual mongooses were sometimes seriously wounded by members of the opposing pack. Despite the intense aggression usually directed towards individuals from rival packs, members of different packs were occasionally seen mating with each other, and the rate at which packs met each other increased when females in one or both packs were in estrous. Extra-group copulation was observed under three circumstances: (i) in the middle of fights in

areas of overlap between the home ranges of two neighboring packs; (ii) when males from a neighboring pack intruded into the home range of packs whose females were in estrous and copulated with them; and (iii) when estrous females led their pack deep into a neighboring pack's home range and mated with the males there. In an experiment, subordinate males were the first to investigate caged 'intruders' placed in their home range, spent the most time around intruders' cages, and were most aggressive towards the foreign animals, particularly the males.

It seems therefore that both males and females actively seek matings with members of neighboring groups. For males, extra-group matings are likely to be an effective way of increasing their reproductive success, since any offspring sired in this way will be reared by the members of the rival pack. Somewhat surprisingly, subordinate males were more likely to inspect intruders than dominants. Dominant males responded to the presence of foreign animals by guarding the breeding females in the group, perhaps because they have more to lose (in terms of paternity) than subordinate males, should the females in their pack copulate with males from a rival group. Preventing females from mating with foreign males will be particularly important for dominants if extra-group copulation by pregnant females causes them to abort, in a manner similar to the 'Bruce effect' in mice (Bruce 1960). This suggestion is strengthened by the observation that females that were suspected of being pregnant came back into estrous after mating with foreign males. Subordinate males, by contrast, may have a stronger incentive to mate opportunistically with females from other packs as they apparently have little chance of obtaining paternity within their own group (Cant 2000). Forthcoming genetic data should reveal the degree of reproductive skew among males within the group, and the frequency with which females obtain extra-group fertilizations.

It is less clear why females should accept and even actively encourage such extra-group matings. Females are unlikely to obtain an advantage in the form of good genes, since there are usually a large number of males in their own group with whom a female could mate. Our observations suggested that little comparison or evaluation preceded a female's choice of extra-group mating partner. One suggestion, arising from studies of primates, is that females mate with males of neighboring groups to reduce the probability of infanticide by those males in the future (van Noordwijk 1985; Wrangham 1997). Extra-group infanticides by males are rare in mammals, but have been observed in chimpanzees, gorillas, coyotes, and banded mongooses (Camenzind 1978; Struhsaker & Leland 1983; Packer & Pusey 1984; Cant 1998). It is interesting that in two of these species, chimpanzee and banded mongoose, females apparently actively seek copulations with males from neighboring groups (Gagneux et al. 1997; this study). In the banded mongoose, however, mating with extra-group males is unlikely to provide a female with effective insurance against infanticide, because neighboring packs may contain up to 20 males, any one of which could potentially kill her offspring during a fight. Moreover, extra-group matings may increase the threat of within-group infanticide by male

pack-mates. Indeed, the only two within-group infanticides observed during the study were both carried out by males (Cant 2000).

Although it is difficult to draw firm conclusions because of our small sample size, it is plausible that females mate with members of other groups to increase the level of heterozygosity among their offspring and avoid the adverse effects of inbreeding, such as the expression of deleterious recessives or increased vulnerability to parasites (Williams 1966; Rood 1975; Hamilton 1993). Inbreeding depression has been repeatedly demonstrated in captive and experimental animals, but there are few data from wild populations (Ralls et al. 1986; Thornhill 1993). Nevertheless, its deleterious effects are suggested by the observation that 35 out of 39 bird and mammal species which live in family groups, and therefore have the greatest opportunities to interact sexually with close kin, show strong tendencies to avoid incestuous matings (Emlen 1995). In cooperatively breeding lions (Packer & Pusey 1993), hyenas (Smale et al. 1993) and wild dogs (Frame et al. 1979), for example, members of the dispersing sex leave the group when potential mates are restricted to close kin.

Inbreeding may be a particular problem for the banded mongoose because both males and females remain in their natal group far past the age of sexual maturity, and some individuals of both sexes are born, reproduce and die all within the same pack (Cant 1998). Constraints on dispersal appear to be high: we observed no emigration or immigration by single individuals over the course of the study, and most individuals left their natal group only after being forcibly evicted en masse by dominants (Cant et al. 2001). However, genetic models suggest that even the occasional introduction of novel alleles into a mating pool is sufficient to prevent loss of heterozygosity through inbreeding (in diploids, around one migrant every two generations, irrespective of population size; Wright 1931; see also Roughgarden 1979, Chapter 12). Extra-group fertilizations in the banded mongoose may therefore be an effective method of reducing the rate at which inbreeding increases homozygosity within the group. It must be noted, however, that dwarf mongooses, in which there are similar constraints to dispersal, commonly inbreed, but there is no evidence that this leads to reduced offspring fitness (Keane et al. 1996). Why selection should favor inbreeding avoidance behavior in one species but not the other remains unclear. Future genetic data will allow a test of the hypothesis that inbreeding entails greater costs in banded compared to dwarf mongooses.

Relations between packs are less aggressive in other social mongooses, and inter-group mating is observed only rarely. In dwarf mongoose, encounters between groups are usually brief and involve chasing and vigorous anal marking of objects. Physical contact and biting occurs only occasionally (Rood 1986). Mating between members of different dwarf mongoose groups has never been observed, and DNA fingerprinting of 45 offspring revealed no evidence of extra-group paternity (Keane et al. 1994). In suricates, encounters between groups occur less frequently than in banded mongooses, and rarely lead to physical contact (Russell, pers. comm.). On rare occasions males have been observed to visit neighboring groups and mate with subordinate females, but there is currently

no information about whether these copulations lead to fertilization (Russell, pers. comm.). Again, it is not yet known why these differences exist. Forthcoming genetic analyses and longer-term demographic data on banded mongooses will facilitate a comparison of patterns in breeding and extra-group mating behavior with those of dwarf mongooses and suricates (e.g. Creel & Waser 1994, 1997; Keane et al. 1996; Clutton-Brock et al. 1998, 2000, 2001).

We do not yet know whether the increase in encounter rate during estrous is primarily due to the behavior of males or females. Females usually lead the group on foraging trips (De Luca & Ginsberg 2001), and are probably well placed to instigate many of the encounters which occur during estrous. Observations of male forays, however, raise the interesting possibility that males remotely monitor the reproductive status of females in neighboring groups using cues in their scent. Both male and female banded mongooses will vigorously scent-mark cloth that has been marked previously by unfamiliar individuals (Cant, unpubl. obs.), providing an opportunity to perform experiments in the future to determine the information content of scent markings. Accurate mapping of foraging routes in estrous and non-estrous periods would also help to evaluate the relative importance of male and female behavior in promoting inter-group encounters during estrous.

Acknowledgements

We thank the Uganda Wildlife Authority for permission to work in Queen Elizabeth National Park, and the Uganda Institute of Ecology, Chief Park Warden Latif Amooti and Henry Busulwa for logistical support at the study site. For help in the field, we thank Daniela De Luca, Jason Gilchrist and Onen Marcello. Thanks to Peter Brotherton, Tim Clutton-Brock and two anonymous referees for comments on an early version of this paper, and to Justin O'Riain for advice and help with the experiments. Financial support was provided by awards from the Biotechnology and Biological Sciences Research Council, Sigma Xi, ASAB, Worts Travelling Scholars Fund, St Catharine's College, and the Department of Zoology, Cambridge (to M.C) and a World Wildlife Fund Prince Bernard Scholarship (to E.O).

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Received: May 15, 2001

Initial acceptance: November 21, 2001

Final acceptance: January 30, 2002 (J.-G. Godin)