

Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*)

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Abstract

The mode by which individuals disperse, and the cost of dispersal, are of great importance in attempts to understand variation in reproductive skew in animal societies. In this paper we report detailed information on dispersal and pack formation in banded mongooses *Mungos mungo*. Six pack fission events were recorded among 11 packs over 22 months. Pack fission occurred under two distinct circumstances. First, groups of individuals were evicted from their natal group as a result of intense aggression from other group members. A small fraction of group members was responsible for most of the aggression. Both sexes helped to attack and evict individuals from the group, and both males and females were driven out of their natal groups *en masse*. The second mode of pack fission occurred when groups of same-sex individuals left their natal group voluntarily to join dispersing individuals of the opposite sex, thereby forming new packs. Dispersing groups were more frequently involved in fights with rival packs of mongooses compared to established groups, and in one instance these fights seemed to be responsible for severe injury and increased mortality among members of a dispersing group. The observations of eviction provide one line of evidence that the presence of subordinates is sometimes detrimental to dominants, contrary to the assumptions of concession models of reproductive skew.

Key words: co-operative breeding, reproductive skew, delayed dispersal, aggression, *Mungos mungo*

INTRODUCTION

Recent interest in co-operative breeding has centred on reproductive skew, which measures the evenness with which reproduction is distributed among the members of an animal society or group. This interest has been stimulated by the development of ‘concession’ models of reproductive skew which are based on the idea that subordinates remain in groups only if they have (or are given) immediate fitness incentives to do so (for concession models see Vehrencamp, 1979, 1983; Reeve, 1991; Reeve & Ratnieks, 1993; Cant & Johnstone, 1999; Johnstone *et al.*, 1999; Kokko & Johnstone, 1999; for empirical tests in vertebrates see Creel & Waser, 1991, 1997; Reeve & Keller, 1995; Emlen, 1997; Jamieson, 1997). These models assume that dominants have full control over breeding within the group, but may sometimes gain from relinquishing a share of reproduction to subordinates as an inducement for them to remain in

the group and help with offspring care rather than disperse.

The relevance of these models to social vertebrates has recently been called into question for two reasons (Cant, 1998; Clutton-Brock, 1998; Clutton-Brock *et al.*, 1998; Johnstone & Cant, 1999). First, in birds and mammals it remains unclear whether dominants do have perfect control over the distribution of subordinate reproduction, or whether subordinates often reproduce simply because dominants are unable to prevent them from doing so. The presence of subordinates may therefore represent an unwelcome threat to the dominant’s reproductive monopoly. Second, long-lived animals may derive their own benefits from delaying dispersal, whether or not this behaviour is in the dominant’s best interest. For example, subordinates may enjoy a number of ‘future’ benefits such as enhanced survivorship or access to resources, the inheritance of all or part of the parents’ territory, membership of coalitions in which to disperse, and the acquisition of experience which increases the helpers’ own breeding success later in life (Gaston, 1978; Wiley & Rabenold, 1984; Emlen, 1991; Koenig *et al.*, 1992; Lucas, Creel & Waser, 1997). Often,

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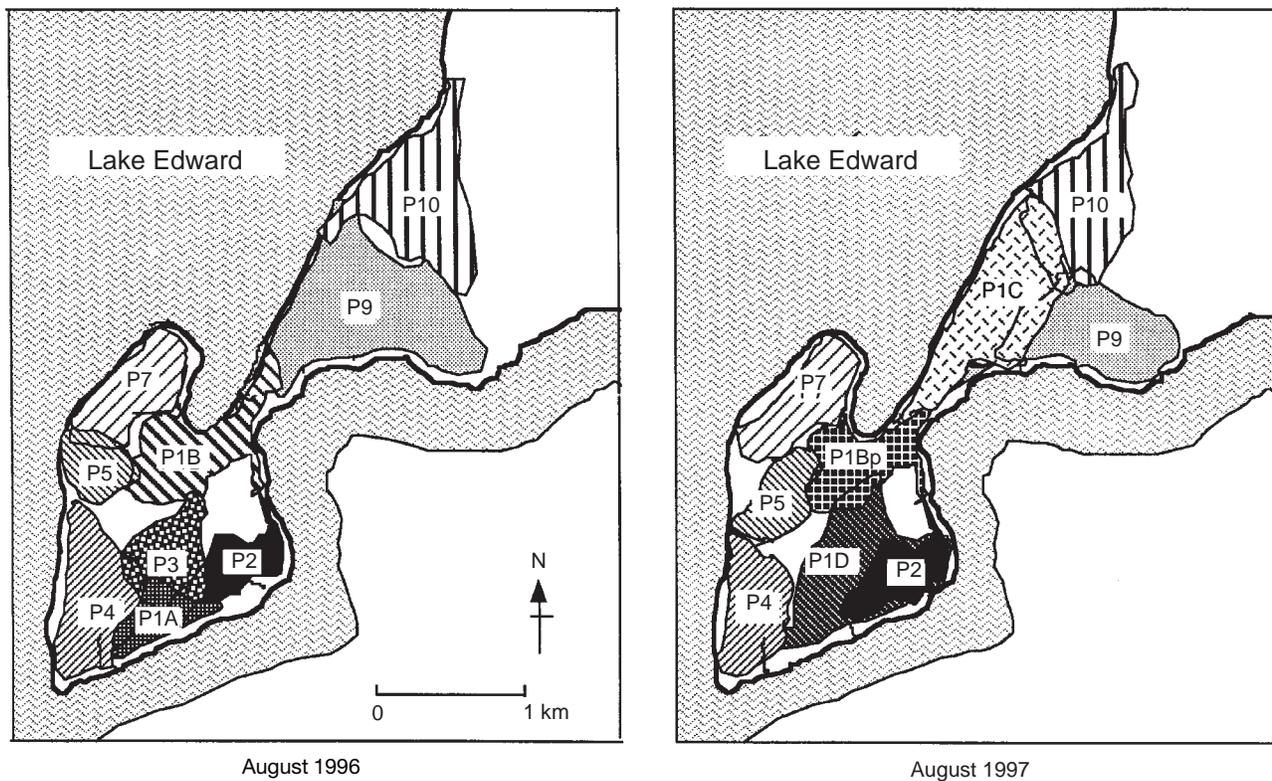


Fig. 1. Map showing the approximate home ranges of banded mongoose *Mungos mungo* packs on and around Mweya peninsula, Uganda in August 1996 and August 1997.

therefore, subordinates may prefer to remain in their natal group while at the same time dominants would prefer them to depart.

This view is supported by the fact that, in numerous co-operatively breeding vertebrates, dominants forcibly evict subordinates from the group, while the subordinates themselves are clearly reluctant to leave (see Johnstone & Cant, 1999 and references therein). Forcible eviction is not expected from the perspective of simple concession models, since the dominant should be able to impel unwelcome subordinates to disperse simply by monopolizing reproduction. Eviction is expected, however, where dominants do not have full control over reproduction. In a recent alternative to concession theory, Johnstone & Cant (1999) argue that the threat of eviction may often be the sole means by which dominants can exert influence over the level of subordinate reproduction. In such cases subordinates who benefit from group membership (for instance, because they have little hope of dispersing successfully) will be selected to exercise a degree of reproductive restraint so as not to trigger eviction by the dominant.

Accurate information concerning the mode by which subordinates disperse (e.g. whether dispersal is voluntary or the result of intense aggression by dominants), is therefore of central importance in deciding which type of model will be most useful in attempts to understand the causes of variation in skew in a particular species or group of species. Here we describe in detail the pattern and mechanisms of dispersal in male and female banded

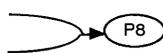
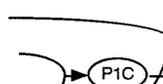
mongooses *Mungos mungo*. Banded mongooses are small (*c.* 1.5 kg), diurnal viverrids that live in highly co-operative groups of around 20 individuals. Up to seven females may give birth together in a communal den, and both males and females help to guard and provision the pups (Rood, 1974; Cant, 2000). In a previous study of banded mongooses, Rood (1975) described the formation of new packs by the fission of existing groups. Rood did not observe pack splits directly, however, and no information was available on the causes of the splits, nor about the age, sex or fate of dispersing animals.

METHODS

Data were collected on dispersal and pack fission on a population of 341 banded mongooses living on and around Mweya peninsula, Queen Elizabeth National Park, Uganda, between November 1995 and August 1997. Mweya peninsula is a 4.95 km² promontory extending into Lake Edward, connected to the mainland by a narrow isthmus (Fig. 1). The habitat is medium-height grassland (principally *Sporobolus pyramidalis* and *Chloris* spp.) dotted with *Euphorbia candelabrum* trees and thickets of *Capparis tormentosa* and *Azima tetra-cantha* (see Spinage, 1982; Cant, 2000). The peninsula is divided into 'lower' and 'upper' areas by a *c.* 40 m-high grassy fault running the length of the land mass.

Ninety-five per cent of the individuals in the popula-

Table 1. Incidences of pack fission between November 1995 and August 1997. 'Forced' splits were those in which animals were repeatedly attacked until they left the group; 'voluntary' splits were those where animals left their pack to join a dispersing group of opposite-sexed individuals, thereby forming a new pack. P, Pack

Pack	Date	No. dispersing	Sex	No. same sex remaining	Forced/voluntary	Joinings/pack formation	Dispersal distance (km)
P7	Feb 96	5 ^a	?	?	?		> 10
P5	Feb 96	3 ^a	M	2	?		
P1B	Dec 96	11	M	10	Forced		< 1
		16	F	4	Forced		< 1
P9	Jan 97	11	M	4	Voluntary		
P3	Feb 97	2	F	0	Voluntary		
P1C	Mar 97	5	F	11	Forced	+8 → 	> 23

^a Inferred from the simultaneous disappearance of three males from P5 and five animals of unknown sex from P7, and from the subsequent trapping of one of the missing P5 males in P8.

tion were trapped and marked with colour-coded plastic collars. In addition, 1 or 2 animals in each pack were fitted with a radio-collar (Telonics Ltd, Mesa, Arizona, U.S.A.) with a 20 cm whip antenna. The radio-collar, weighing 27 g, was fitted to adult individuals weighing > 1350 g, and therefore represented a maximum of 2% of an adult's body weight. Details of the trapping and immobilization procedure are given elsewhere (Cant, 2000). Individuals of known age were classed as adults if > 1 year old, subadults if between 6 and 12 months old, and pups if < 6 months old. We further divided adults into 6 age classes using tooth wear. Males were classed as 'dominant' and 'subordinate' depending on whether they had mate-guarded females during oestrus (see Cant, 2000 for details).

Home ranges were estimated by plotting the location of packs and their dens on an aerial photograph of the study area, divided into 1 ha 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 faeces at each visit. Home ranges were plotted by drawing straight lines between the most peripheral dens or marking posts used during the study. The home range of some packs changed between 1996 and 1997 (see Fig. 1) so for these packs an average home-range area for the 2 years was calculated. Pack size was measured each month. Modal pack size was calculated as that size at which the pack spent the greatest number of months, consecutive or not.

Four packs were habituated to the extent that we could follow them on foot at a distance of a few metres. We recorded the behaviour of individuals in these packs on checksheets using a combination of 10-min focal watches and 5-min scans. Checksheets were designed to include both instantaneous and continuous recording of behaviour (Martin & Bateson, 1993). Typically, habituated packs would be followed in morning and afternoon sessions lasting c. 3 h. Five other semi-habituated packs would tolerate a stationary observer at a distance of

15 m. Behaviour was recorded *ad libitum* from these packs for as long as they remained in view.

Habituated packs were followed for between 2 and 8 h every day before, during and after pack fission, allowing detailed information on the dynamics of the splitting process to be collected. Within a few days of the start of a fission event, we trapped 1 or 2 individuals in a dispersing group and fitted them with a radio-collar. The dispersing animals were then followed every 1 or 2 days until they formed a new pack and settled into a new home range, or, in 2 cases until they dispersed far away from the study area and were lost. The exact age of dispersing animals was known in 2 of 4 examples of pack fission; the age of dispersing animals of the other 2 was estimated by comparing their tooth wear with that of known-age adults.

To measure the frequency with which packs were involved in fights with other packs of banded mongooses, we counted only those occasions that a pack fought another pack while it was being followed by an observer for a morning or afternoon session. The opposing pack was not scored as having been involved in a fight (unless a second observer was following it at the time). The frequency of fighting for a pack was then calculated as the number of fights while being followed divided by the number of mornings or afternoons on which the pack was followed. Non-parametric tests follow Siegel & Castellan (1988); parametric tests follow Sokhal & Rolf (1995). All tests are two-tailed.

RESULTS

Nine packs on Mweya peninsula were visited and censused an average of 125 times each (range 35–314) between June 1996 and August 1997. Estimated home range area of these nine packs averaged 68.5 ± 7.1 ha (mean \pm SE). The average modal pack size of these nine packs was 18.0 (IQR = 9.25) individuals, plus 2.0 (IQR = 5) pups/infants under 6 months old (Cant, 2000). Pack size did not differ in 1996 and 1997 (August

1996: $n=9$ packs, median pack size = 18.0 (IQR = 14); August 1997: $n=9$, pack size = 17 (IQR = 8.5); Mann–Whitney U -test: $U' = 45.5$, NS). Home-range area increased with pack size (Spearman rank correlation: $r_s = 0.72$, $n = 9$, $P < 0.05$).

Incidences of pack fission

Six pack fission events occurred in the study population between November 1995 and August 1997 (Table 1). Two of these splits were inferred to have taken place when the appearance of a new pack on the lower peninsula coincided with the disappearance of animals from two known packs in the same area. This new pack spent 2 months on the lower peninsula, during which time it was attacked on several occasions by larger, neighbouring packs. The day after one particularly vicious attack, the new pack dispersed away from the peninsula and was lost.

The other four pack splits were observed directly when known marked animals were evicted from habituated packs, followed by known marked animals leaving other packs to join them. By far the most detailed information on pack fission was collected on two of these splits, which occurred in habituated packs during the course of the study. These are described in detail below. Figure 1 shows the approximate home ranges of packs on and around Mweya peninsula in August 1996 and August 1997.

Pack 1B split, December 1996

In December 1996, pack 1B consisted of 20 females (five of which were pregnant) and 21 males (not counting individuals < 6 months old). The oldest female gave birth on 16 December, whereas the other four pregnant females did not give birth until 2 days later. This contrasts with the usual pattern, in which all females in a pack give birth on the same day (Cant, 2000). The oldest females in the pack came into oestrus on 23 December, and mating and mate-guarding continued over the next 2 days. When the pack was visited the following morning (26 December or Day 1), the animals were behaving in a highly agitated manner and there was a sudden increase in the level of aggression (Fig. 2). Some animals repeatedly attacked others, delivering bites to the face, body and legs in the same manner with which they would fight against members of a foreign pack.

Of 45 aggressive acts recorded during the split, 13 involved groups of males and females attacking other small mixed-sex groups, 11 were attacks by males on other males, five were attacks by males on females, and two were attacks by females on other females. Some individuals were much more aggressive than others. Of the 17 individuals > 6 months old who remained in Pack 1B after the split, five individuals, all males, were responsible for 87% of aggressive attacks. The most aggressive individual, a dominant male, was responsible

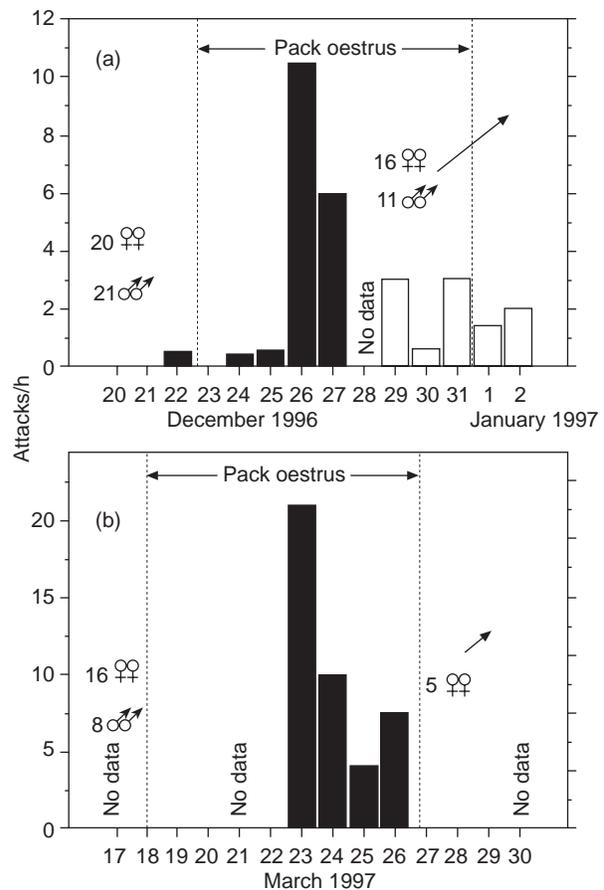
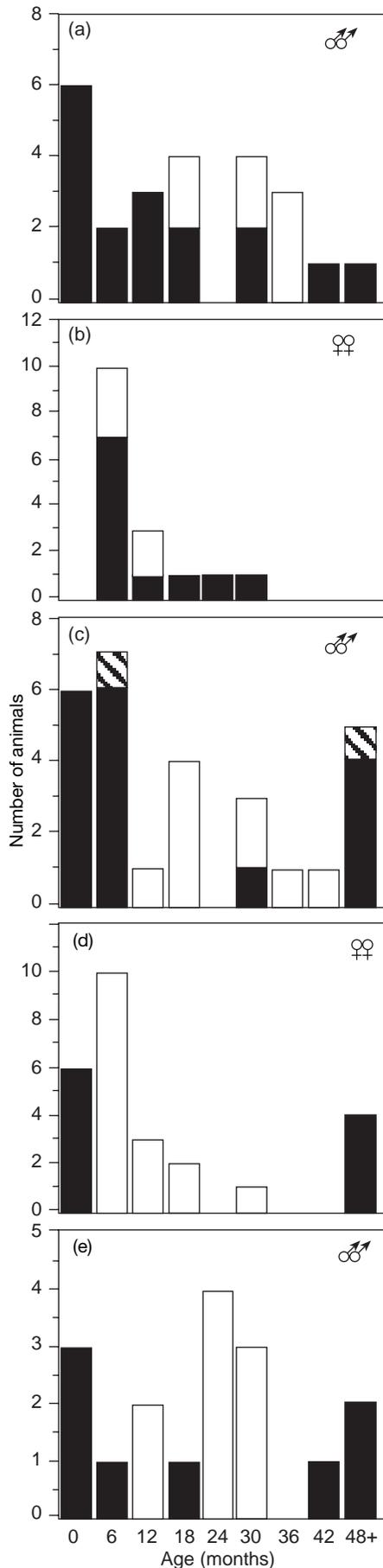


Fig. 2. Changes over time in the rate of aggressive attacks of banded mongooses *Mungos mungo* during pack fission. (a) Pack 1B split, December 1996. White bars, attacks directed toward two males who were eventually reaccepted into the pack. (b) Pack 1C split, March 1997. The composition of the pack before the split is shown to the left of each graph; the number and sex of evicted animals is shown below an arrow on the right of each diagram. The region between the vertical dotted lines shows the period for which females in the pack were in oestrus.

for 35% of the total number of attacks. Two of the five most aggressive individuals were dominant males while the other three were subordinate males.

By Day 3, 27 individuals had been evicted from pack 1B. These individuals formed two distinct splinter groups according to sex. One group comprised 16 young females (including three breeding females) (group F); the other group comprised 11 males (group M). The female group occupied an area of the peninsula close to their parent pack and were involved in sporadic fights with neighbouring resident packs. On day 11, the 16 females in group F were joined by 11 adult males who dispersed from one of these neighbouring packs. Within 4 h of joining group F, the new males were seen fighting against members of their former (natal) pack. The newly formed pack took up a home range just north of the neck of the peninsula. Over the next 2 weeks, three of the joining males returned to their natal pack and were eventually accepted.



The male splinter group (group M) took up a loosely defined home range on the upper peninsula. On day 32, a new pack was formed when these males were joined by two females from the smallest pack on the peninsula. A single, previously unknown male also joined the pack at this time.

Pack 1C split, March 1997

In March 1997, pack 1C consisted of eight males and 16 females, 10 of whom were < 12 months old. The pack came into oestrus on 18 March, and was visited at least once every day (except one) for the next 12 days. Mating was observed on every day up to the 26 March. On the morning of the 23 March (day 1), however, there was a sudden increase in the level of aggression (Fig. 2b). Certain young females in the pack were repeatedly attacked by older females in the group. Of 36 attacks observed over 4 days, 32 (89%) were attacks on females by other females and four (11%) were attacks by males on females. There were no attacks on males by either males or females. The four oldest females in the pack carried out 87% of the attacks, with one female accounting for 51% of the attacks on her own. After 2 days of being repeatedly chased and bitten, two young females, both < 12 months old, were limping badly and lagging 20 or 30 m behind the rest of the pack. By Day 4, three other young females had been evicted, and these five females were sleeping in a den 500 m away from the rest of the pack.

By Day 7, the five evicted females had dispersed 11 km away from Mweya. They were last seen on Day 33, 23 km to the north-west of Mweya, by which time they had been joined by eight other, unknown animals. This new pack was subsequently lost.

Age and sex of dispersing animals

Both males and females who were evicted tended to be of intermediate age, usually between 1 and 3 years old (Fig. 3). Animals < 6 months and > 48 months old were not evicted (with the exception of one old male in pack 1B, who was later reaccepted into the group; Fig. 3c). Similarly, the males who voluntarily dispersed to join the 16 females evicted from pack 1B were of intermediate age: no males > 36 months old or < 12 months left pack 9 (Fig. 3d). Comparison of rates of

Fig. 3. Age distribution of banded mongooses *Mungos mungo* who were evicted from the group (□) or who remained in the group (■) during pack fission. (a) Pack 1 split, September 1995 (males only evicted); (b) pack 1C, March 1997 (females only evicted); (c) and (d) pack 1B, December 1996 (both males and females evicted), (▨), two males who were initially evicted but were later reaccepted into the group; (e) Age distribution of males who dispersed voluntarily from pack 9 in January 1997 to join the females evicted from pack 1B in December 1996.

dispersal of males and females is difficult because detailed information on the age and origin of animals was not available before 1996. In one well-studied pack, however, 14 out of 18 surviving males and three out of seven surviving females were evicted by the age of 3 years (G -test: $G_1 = 2.47$, NS). The four males who did not disperse all attained dominant status in their natal packs by the age of 2 years. All seven females had reproduced by the age of 2 years, whether or not they remained in their natal packs.

Cost of dispersal

Because home ranges in the study area were contiguous or overlapping, new packs attempting to establish a home range on or around the peninsula encroached upon the range of other packs. This led to frequent fights between packs. In the first month after dispersing, newly formed packs fought more than four times as frequently as 'resident' packs, which we defined as established packs that had contact only with other established packs (dispersing packs: $n = 4$, median = 0.239 encounters/following session; residents: $n = 7$, median = 0.058 encounters/session; Mann–Whitney: $U' = 26$, $P < 0.05$).

Observations of the attempt of one newly formed pack to establish a home range in an area used by a larger, resident pack suggested that such frequent encounters can be costly for members of dispersing packs. In the first 3 months after dispersal, the new pack was observed fighting with its larger rival 17 times out of the 71 times that the pack was followed. After one such fight in February 1997, a dominant male in the new pack was seen bleeding from the mouth; he subsequently disappeared. Another male disappeared 2 weeks later. In March 1997, one of the females received a deep wound to her hind leg, typical of the type of injury inflicted by other mongooses. After a fight in April 1997, a male was found with wounds to the back legs and a fractured forelimb; another could barely walk and disappeared within days. A dominant male disappeared in May 1997 and was presumed dead. Of the 12 males present in the new pack when it formed in January 1997, only eight remained 7 months later, when the study ended. This mortality rate (0.33) was significantly higher than that of adult males in seven other resident packs over the same period (0.12; G -test: $G_1 = 3.56$, $P < 0.05$).

DISCUSSION

Our results indicate that there are two distinct modes by which banded mongooses emigrate from their natal groups. First, groups of males, females or both were sometimes driven out of their natal groups as the result of intense aggression from other group members. The primary agents of this aggression were dominant males and females, but subordinates of either sex also contributed to driving individuals out of the pack. In one split,

males carried out most of the attacks, directing their aggression at both males and females; in another split, females were the main aggressors, directing their attacks exclusively at other females. When both males and females were evicted from a pack at the same time, the dispersing animals immediately separated into same-sex groups and went separate ways.

The second mode of emigration was apparently voluntary, and occurred when groups of same-sex individuals left their natal group to join members of the opposite sex that had been evicted. The results suggest that animals of intermediate age (between 1 and 3 years old) are most likely to disperse, whether this is forced or voluntary.

Newly formed packs sometimes attempted to establish home ranges immediately adjacent to that of their natal pack, but were also observed to disperse over distances > 20 km. The attempt by new packs to establish home ranges in areas already occupied by banded mongooses led to an increased rate of fighting between packs, and to an increased rate of mortality among dispersing individuals. Despite leaving their natal group in large, same-sex coalitions, dispersal apparently involves substantial costs to banded mongooses, with one of the greatest threats to dispersing animals coming from attacks by resident groups of conspecifics.

Why do banded mongooses sometimes leave their natal group voluntarily, and why are they sometimes evicted? It is difficult to draw firm conclusions because of the small number of dispersal events for which information was available, but the results suggest several possibilities. Considering voluntary dispersal first, it seems probable that banded mongooses leave their natal packs voluntarily to gain improved access to suitable mates, as has been shown in dwarf mongooses (Rood, 1986, 1990; Creel & Waser, 1994). In contrast to dwarf mongooses, however, this occurs by the formation of new packs rather than by immigration into established groups. Three males emigrated from a pack containing more breeding females than adult males, which suggests that factors other than the simple availability of opposite-sex adults (e.g. inbreeding avoidance) may play a role in the patterns of dispersal. Inbreeding may be a particular problem for banded mongooses, since the tenure of dominant males and breeding females is longer than the time taken for their offspring to reach sexual maturity (see Clutton-Brock, 1989). Forthcoming genetic data may reveal whether individuals who disperse are more closely related to opposite-sex breeders than those who remain in their natal group.

Second, what are the reasons underlying the forced eviction of males and females from their natal packs? Both eviction events observed here occurred in packs that were considerably larger than the average (one occurred in a pack which comprised 59 animals, the largest number of individuals seen at Mweya by either Rood (1975) or ourselves), suggesting that eviction may be used to reduce overly-large groups (although there is currently no evidence that per capita productivity or

survivorship declines in the largest groups). Alternatively, it may be increases in the number of potential breeders, rather than the number of animals *per se*, which leads to eviction. The fact that both observed evictions (plus one other eviction event recorded just before the start of this study; D. De Luca, pers. comm.) occurred during oestrus suggests that eviction may be linked to direct competition between breeders. It is worth noting that the one incidence where females evicted other females occurred in a group containing 16 females, all of whom would have been sexually mature within 6 months. Where dominants have little or no ability to suppress reproduction in females, eviction of females may be the only way of regulating the number of young born in a group. This may help to explain the rather puzzling observation that dominant males helped to evict sexually mature females from the group.

Information on the mode by which subordinates disperse provides one way of evaluating whether the assumptions of a particular model of reproductive skew are likely to hold for the species under consideration. This sort of evaluation should precede any attempt to test the predictions of a model or class of models. The results presented in this paper represent further evidence that the assumptions of concession models do not apply to banded mongooses (see also Cant, 2000). Forcible eviction is not expected from the perspective of concession models, since these models assume that subordinates are retained only when this is in the dominant's best interest, and that the presence of subordinates cannot threaten the dominant's reproductive monopoly. Rather, the results provide one line of evidence that the presence of subordinate animals can be detrimental to the fitness of dominants, and that their expulsion may be a means by which dominants attempt to protect their reproductive interests. We suggest, therefore, that models of skew based on incomplete control (e.g. Cant, 1998; Reeve, Emlen & Keller, 1998; Johnstone & Cant, 1999) may be of greater use in understanding the distribution of reproduction in this species.

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