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Social control of reproduction in banded mongooses

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Recent theoretical work suggests that the distribution of reproduction, or degree of reproductive skew, in animal societies depends crucially on (1) whether dominant individuals can fully control subordinate reproduction, and (2) how subordinate reproduction affects the fitness of dominants. I investigated these two factors in cooperatively breeding banded mongooses, *Mungos mungo*. Female packmates entered oestrus together and were closely guarded by dominant males. These males were aggressive to subordinate males who attempted to mate, but females still managed to mate with males other than their mate guard. Older females were guarded and mated a few days before their younger packmates, yet all females usually gave birth on the same day, suggesting that older females may have a longer gestation period. Moreover, older females carried more fetuses. Overall, ca. 83% of adult females conceived in each breeding attempt and 71% carried to term. These results indicate that, among males, dominant individuals did not have full control over the mating attempts of subordinates (since they could not fully control the mating behaviour of the females they guarded), while among females there was little or no attempt to prevent subordinates from breeding (at least, prior to parturition). Two within-group infanticides by males suggested that some control over reproduction may be exercised postpartum. Per capita survivorship of young in the den increased with the number of females who gave birth. Thus, dominant females may benefit from subordinate reproduction, providing a possible explanation for the lack of reproductive suppression among females in this species.

Social animals vary greatly in the evenness with which reproduction is distributed among group members. This characteristic of animal societies is called reproductive skew (Vehrencamp 1979, 1983a, b; Reeve 1991; Keller & Reeve 1994). Interest in reproductive skew has been stimulated by the development of simple mathematical models that attempt to account for variation in the way reproduction is shared among the members of animal societies, from high-skew societies in which one or a few individuals monopolize reproduction, to low-skew societies in which reproduction is shared more equitably.

Models of reproductive skew fall into two broad classes. 'Concession' models (Vehrencamp 1979, 1983a, b; Reeve 1991; Reeve & Ratnieks 1993; Cant & Johnstone 1999; Johnstone et al. 1999; Kokko & Johnstone 1999) assume that the distribution of reproduction between group members is under the full control of a single dominant individual. Dominants are further assumed to benefit from the presence of subordinates, and so may gain by conceding a share of reproduction (or 'staying incentive') to these subordinates to induce them to remain in the group. Recently, however, the assumption of full control by dominant animals has been called into question (Cant 1998; Clutton-Brock 1998), leading to the development of a number of different 'incomplete control' models in which this assumption is relaxed (Cant 1998; Reeve et al. 1998; Johnstone & Cant 1999a, b). Thus, the question of how and to what extent dominants control the reproduction of their subordinates lies at the heart of theoretical efforts to understand the partitioning of reproduction in animal societies.

But what is meant by dominant control of subordinate reproduction, and what form might this control take? Among mammals, dominant males are usually seen to assert control over reproduction through conspicuous forms of behaviour such as mate guarding (e.g. Rood 1980; Packer & Pusey 1982), or the physical punishment of subordinates who attempt to mate (reviewed by Clutton-Brock & Parker 1995). Among females, by contrast, sexually mature subordinates often fail to reproduce, and are said to be 'reproductively suppressed', without it being known whether this reflects social control by a dominant (as the term 'suppression' might imply) or is simply a consequence of differences in nutritional status or body condition (reviewed in Wasser & Barash 1983; Creel & Macdonald 1995; Woodroffe & Macdonald 1995; French 1997; Clutton-Brock 1998).

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Overt acts of aggression and infanticide are clear indications that dominants exert control over the distribution of reproduction. However, Keller & Nonacs (1993) argued that the threat of physical punishment or infanticide must also underpin other, more subtle mechanisms of reproductive control (such as the production of pheromones that inhibit reproduction), or else subordinates would be expected to evolve physiological countermeasures. Thus, the extent to which a dominant female can control reproduction within her group will ultimately depend (as it does for males) on her physical ability to reduce the net benefits of breeding to subordinates, for example by killing their young, even if such acts are rarely observed (Hrdy & Hausfater 1984; Johnstone & Cant 1999b). The ability to use infanticide or physical attacks on offspring as a weapon of suppression, however, is likely to be constrained by the difficulty of distinguishing between one's own young and those of a rival. For males, determining the parentage of young is always likely to be difficult (discussed in Davies 1992; Pagel 1997). In communally breeding species, in which the offspring of different mothers are reared together, females too may find it hard to identify their young, since in these circumstances the spatial and temporal clues to offspring identity that might be used under other circumstances will be of little use (Johnstone & Cant 1999b).

In this paper I investigate variation in breeding success among male and female banded mongooses, *Mungos mungo*, the extent to which dominant males and females exert control over the reproductive efforts of subordinates, and the methods by which such attempts at control might be evaded. I then use this information to assess the applicability of skew models to explain the distribution of reproduction in this species. Banded mongooses are small (ca. 1.5 kg), diurnal viverrids which live in mixed-sex groups of ca. 20 individuals, feeding on beetles, millipedes and small vertebrates. Reproduction is synchronized within but not between packs, and it is the norm for several females to give birth together in the same breeding den (Neal 1970, 1971; Rood 1975). As such they are often used as a rare example of a low-skew mammalian society (e.g. Reeve & Keller 1995; Sherman et al. 1995; Emlen 1997). Pups remain in the den for 3–4 weeks after birth, and both males and females help to babysit young at the den during this time (Rood 1974, 1975, 1986). Pups emerge from the den and start to accompany the rest of the group on foraging trips at ca. 4 weeks old, and both sexes help provision the pups for up to 8 weeks after emergence (unpublished data). Pups are suckled by any lactating female, apparently without discrimination (Neal 1971; Rood 1975, 1986).

METHODS

Study Area and Study Population

I collected data on a population of 341 known individuals living in 14 packs on and around Mweya peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E), between November 1995 and August 1997. The habitat around Mweya peninsula is medium-height grassland (principally *Sporobolus pyrimidalis* and *Chloris* spp.) dotted with *Euphorbia candelabrum* trees and thickets of *Capparis tormentosa* and *Azima tetracantha* (Spinage 1982). The peninsula is divided into lower and upper halves by a grassy fault ca. 40 m high. Major herbivores at the site are hippopotamus, *Hippopotamus amphibus*, warthog *Phacochoerus aethiopicus*, waterbuck, *Kobus ellipsipyrimus defassa*, buffalo, *Syncerus caffer*, and elephant, *Loxodonta africana*. Common predators include hyaena, *Crocuta crocuta*, lion, *Panthera leo*, leopard, *Panthera pardus*, martial eagle, *Polemaetus bellicosus*, bateleur eagle, *Terathopius ecaudatus*, and black-chested snake eagle, *Circaetus pectoralis*. Annual precipitation is typically 800–900 mm, with two dry periods in January–February and June–July each year (Rood 1975). Information on rainfall at Mweya was available throughout the study courtesy of Uganda Institute of Ecology Meteorological Station.

Table 1. Banded mongoose packs studied on and around Mweya peninsula between November 1995 and August 1997

Pack	Period of study	Group size (adults+subadults) Mode	Minimum	Maximum
P1A	Nov. 95–Nov. 96*	8	6	10
P1B	Nov. 95–Dec. 97†	24	18	44
P1Bp	Jan. 97–Aug. 97	26	13	27
P1C	Jan. 97–Aug. 97	18	17	27
P1D	Jan. 97–Aug. 97	14	10	15
P1E	Mar. 97–Apr. 97‡	5	4	12
P2	Nov. 95–Aug. 97	25	23	33
P3	Nov. 95–Jan. 97*	6	5	6
P4	Nov. 95–Aug. 97	18	14	21
P5	Aug. 95–Aug. 97	10	7	12
P7	Apr. 96–Aug. 97	21	21	25
P8	Apr. 96–May 96‡	6	5	7
P9	Aug. 96–Aug. 97	14	14	25
P10	Aug. 96–Aug. 97	10	10	12

Group size (number of individuals over 6 months old) was measured each month. Modal group size was that size at which the pack spent the longest number of months, consecutive or not.
*Pack went extinct.
†Pack split and became P1Bp.
‡Pack dispersed away from the study area.

Packs averaged 18.0 (interquartile range, IQR=9.25) individuals (more than 6 months old), plus 2.0 (IQR=5.0) pups/infants under 6 months of age. Table 1 shows the modal, minimum and maximum group sizes of the 14 study packs. The adult sex ratio was male biased: the adult sex ratio within packs averaged 1.8 (males to females), and 11 out of 13 packs in which all adults were sexed contained more males than females. The home range area of nine packs on Mweya peninsula averaged 68.5 ± 7.1 ha ($\bar{X} \pm$ SE). Packs produced an average of 3.6 litters/year, and the average interbirth interval was 88 days (unpublished data). Five of the study packs had potential access to domestic rubbish tips around Mweya peninsula, so I classified packs as ‘provisioned’ or ‘unprovisioned’ for some analyses, according to whether they had access to these supplementary sources of food. I located packs by radiotelemetry and approached them on foot until the animals were sighted.

Trapping and Marking Techniques

Over 95% (325/341) of the population were captured in baited live traps (Tomahawk Inc., Wisconsin, U.S.A.), including all adult members of 11 packs. Trapped mongooses over 6 months were immobilized using a combination of 1.4 mg ketamine (Vetalar: Veterinary Drug Co, York, U.K.) and 1.2 mg medetomidine (Domitor: Veterinary Drug Co) injected into the femoral muscle (unusually small animals and those between 3 and 6 months old were given two-thirds of these doses; animals under 3 months old were not anaesthetized). Individual mongooses were measured, weighed and scored for tooth wear on a scale of 1 (very light) to 7 (very heavy). On first capture, all anaesthetized animals were tattooed with an ID number on the inside of their right thigh. In addition, adults were fitted with colour-coded plastic collars for visual identification. Particular care was taken to ensure that the collars were loose fitting, and the collars were usually replaced every 3–6 months. I marked subadults and infants by shaving a small (ca. 4 cm^2) area of fur from the rump.

Where ages were known, I classed individuals as follows: pups: 0–3 months; infants: 3–6 months; subadults: 6–12 months; adults: over 12 months. Where exact dates of birth were unknown, I classed males as adults if their head width (at the widest point) exceeded 42 mm, and females as adults if their head width exceeded 41 mm. Adults were further divided into six age classes from class 2 (youngest) to class 7 (oldest) on the basis of tooth wear. Within packs, I ranked females according to age, with rank 1 being the oldest. One or two animals of either sex in each pack were fitted with a radiocollar (Telonics Ltd, Mesa, Arizona, U.S.A.) with a 20-cm whip antenna. After processing, mongooses were injected with 1.2 mg atipamezole preparation (Antisedan: Veterinary Drug Co) 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.

Ethical Note

The trapping and immobilization procedure was used 847 times over a 2-year period. No animals died or became sick as a result of this procedure. To avoid possible effects of stress in the later stages of pregnancy, females were usually trapped in the first 2–3 weeks after oestrus, and were not anaesthetized later than 6 weeks postoestrus. Radiocollars weighed 27 g and were fitted only to adult individuals weighing over 1350 g, representing a maximum of 2% of the animals' body weight. The study was carried out under licence from Uganda National Council for Science and Technology and Uganda Wildlife Authority, and the methods used (in particular, the trapping and immobilization procedure) were passed by the Research Division of Uganda Wildlife Authority.

Observations of Mating Behaviour and Definitions

I collected data on mating and mate guarding on six packs using a combination of continuous ad libitum recording and 10-min focal watches of individual animals or male–female pairs. All instances of sexual activity were recorded. A 'mounting attempt' occurred when a male approached an oestrous female, sniffed her perineal region and attempted to lift her tail up with his nose. Females were said to 'accept' the mounting attempt if they stood still, lifted up their tail and rear, and allowed the male to adopt the mating position.

Uninterrupted mountings that lasted for 30 s or more were scored as 'matings'. 'Mate guarding' occurred when one male followed closely behind a particular female for a whole morning or afternoon observation session. This was a conspicuous behaviour and was easily recognized. I scored mate guarding subjectively rather than using objective measures (such as nearest-neighbour distance) because a guarding male could clearly control access to his female even if he was not her nearest neighbour, for example, by allowing females but not other males to approach her. The period from the first to the last observed mating or mate guarding was termed 'pack oestrus'. The duration of the pack oestrous period was measured to the nearest day, whereas the duration for which individual females were mate guarded was measured to the nearest half day.

Patterns of Pregnancy

Pregnancy could be detected visibly in the last 3 weeks before birth. By trapping females, however, I could detect pregnancy by palpation from 2 weeks after oestrus. To test whether females who became pregnant before the age of 12 months were heavier than those that did not, I constructed separate growth curves of weight against age (up to 12 months) for two litters in one habituated pack, and then for each litter calculated the percentage residual weights of females who did and did not get pregnant before 1 year of age. Where females had been weighed several times in their first year, I took the mean of the percentage weight residuals and entered one value for each female into the analysis.

For adult females, I calculated an index of body condition as follows (Kruuk et al. 1987; Woodroffe & Macdonald 1995). Body weight is related to length by the equation $W=aL^n$ where W is weight (g), L is length (cm) and a and n are constants. This equation can be expressed as $\log W=\log a+n \log L$. I estimated the constants a and n for banded mongoose females by fitting a simple linear regression to all data on weight and head–body length of all adult females, excluding those that were pregnant when trapped. This method yielded the values $a=0.015$ and $n=1.917$. I then calculated the expected weight for a given length using the equation given above and condition as observed weight/expected weight. The condition index, therefore, has a mean of 1.

I trapped females 2–6 weeks after oestrus and estimated the number of fetuses per female by gentle palpation of the abdomen. I first located the kidneys in order to exclude them, and then gently explored the rest of the abdomen with both hands. Upon finding a fetus, I held it gently between thumb and forefinger while continuing to search for others. Since I did not have access to an ultrasound scanner I was unable to confirm whether the estimated litter size was the same as the actual number of fetuses carried by pregnant females.

Estimating Gestation Period

The gestation period of individual females was estimated as the number of days from the first day on which a female was mated or mate guarded until the day on which she gave birth. Packs that included females in the later stages of pregnancy were visited every day, usually in both the morning and afternoon. Typically, on the day of parturition, all or most adult females remained in the den in the afternoon while the rest of the pack went to forage. When visited the following morning, it was easy to tell which females had given birth from their weight loss and change in shape. On a few occasions females apparently gave birth in the morning, emerging later in the afternoon to forage briefly. Using these methods the time of parturition could be determined to within 24 h, and sometimes to within 12 h.

Statistics

Because some packs were visited more often than others, or were more habituated, the number of packs used in the following analyses varies. In each case I used the maximum number of packs for which I had data. Means are given ± SE; medians are given with interquartile ranges (IQR). Nonparametric tests follow Siegel & Castellan (1988). Generalized linear regressions were carried out in the Genstat 5 Release 4.1 software package (Numerical Algorithms Group, Oxford, U.K.) assuming binomial errors (for the case where the response variate was proportion of females becoming pregnant) or normal errors (where the response variate was number of emergent pups per pregnant female, after transformation). The modelling procedure used in these regressions followed Crawley (1993). All tests are two tailed.

RESULTS

Female Mating Behaviour

Oestrus among females usually began around 10 days after parturition ($\bar{X} \pm \mathrm{SE}=10.5 \pm 1.5$ days, range 6–24, $N=12$ oestrous periods in seven packs). The onset of oestrus was identified by a sharp increase in the number of mounts attempted by males, and by the start of mate guarding. ‘Pack oestrus’, measured from first to last observed mate guarding or mating, lasted for an average of 6 ± 0.7 days (range 3–10). The duration of pack oestrus was positively correlated with the number of females in the pack (Spearman rank correlation: $r_s=0.936$, $N=10$ oestrous periods, $P<0.01$). In six pack oestrus periods in one highly habituated pack, males attempted to mount all females over the age of 12 months, and 86.5 ± 6.2% of adult females were observed to mate during oestrus.

Females were closely guarded by dominant males during oestrus. Typically, males guarded the same female for 2 or 3 days in a row before moving on to guard a second female in the pack. A mean of 83.5 ± 5.9% of the adult females in a pack were mate guarded for at least 1 day during pack oestrus ($N=12$ pack oestrus periods in seven packs), and individual females were guarded for an average of 2.0 ± 0.2 days (consecutively) of the pack oestrus period (range 1–5). The duration for which females were guarded did not depend significantly on their age class (Kruskal–Wallis: $H_4=4.27$, $N=46$, NS), nor on their age rank (Spearman rank correlation: $r_s=-0.018$, $N=46$, NS). Within packs, there was no significant difference between the oldest and youngest ranking females in the duration for which they were guarded (oldest: median 2.0 days (IQR=0); youngest: median 1.0 day (IQR=2), $N=9$ breeding attempts; Wilcoxon signed-ranks test: $T^+=12$, $N=9$ breeding attempts, NS).

Females appeared to be guarded when they were most receptive. Females accepted 41% (IQR=20) of mounting attempts by males on days when they were guarded compared to 12% (IQR=24) on days in the same oestrous period when they were not guarded (Wilcoxon signed-ranks test: $T^+=28$, $N=7$ females, $P<0.01$). Females were also less frequently aggressive to males in response to mounting attempts on days when they were guarded (percentage of attempts that provoked aggression when guarded=32 (IQR=20); when not guarded=76 (IQR=34); Wilcoxon signed-ranks test: $T^+=28$, $N=7$, $P<0.01$). Seventy-five per cent (IQR=37) of all observed matings involved females who were being guarded that day (Wilcoxon signed-ranks test: $T^+=28$, $N=7$, $P<0.01$). Comparing consecutive days on which females were guarded, there was no significant difference between days in the proportion of mounting attempts that females accepted, nor in the number of observed matings (Kruskal–Wallis tests: percentage acceptance versus day of guarding: $H_2=2.38$, $N=26$, NS; number of matings versus day of guarding: $H_2=3.61$, $N=26$, NS).

There was a significant positive correlation between the age rank of females (with rank 1 being the oldest) and the day of pack oestrus on which they were first mate guarded (Spearman rank correlation: $r_s=0.445$, $N=46$, $P<0.01$; Fig. 1a). Similarly, there was a highly significant positive correlation between females’ age rank and the day on which they were first observed to mate (Spearman rank correlation: $r_s=0.687$, $N=46$, $P<0.001$; Fig. 1b). However, data in these analyses were pooled from 14 oestrous periods in six packs, and sometimes included the same females in the same rank position in consecutive oestrous periods. To counter problems of nonindependence, I calculated the Spearman rank order correlation coefficient (r_s) for the day first mate guarded (or mated) versus female rank in each oestrous period in each pack, and then averaged r_s values for each pack. In all six packs the mean correlation coefficient was positive (one-sample sign test: $P<0.05$). There were too few data on mating in different packs to do a similar test on the correlation between age rank and day of first mating. On average, the

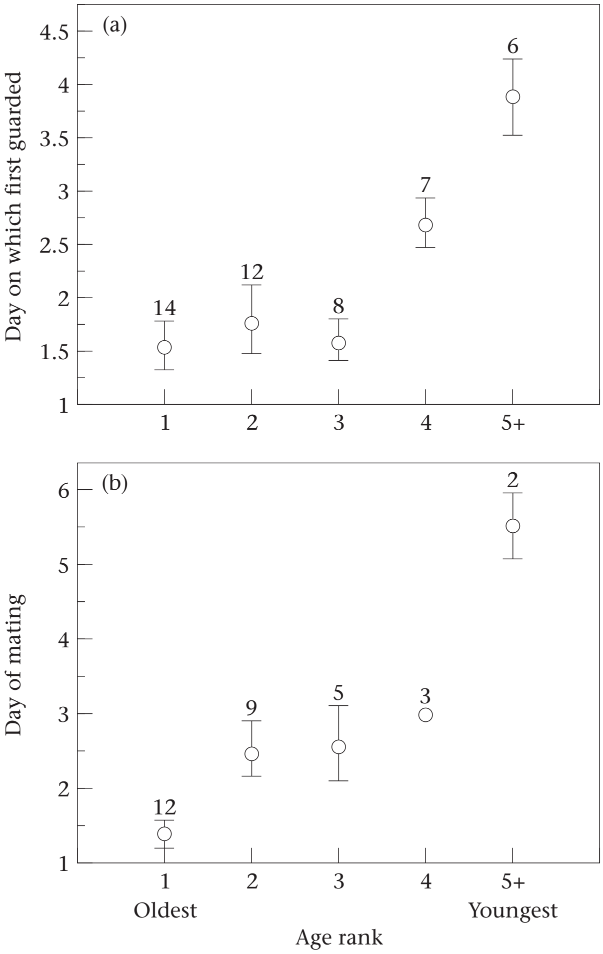

Figure 1. (a) Day on which females were first mate guarded versus their age rank; (b) days on which females were first observed to mate versus their age rank. Day 1 is the first day of pack oestrus, defined as the first day on which either mate guarding or mating was observed. Data are pooled from 14 oestrous periods in seven packs. Means are shown±SE. Numbers above points indicate number of breeding attempts.

lowest-ranking females (rank 5+) were mate guarded for the first time 2.3 ± 0.3 days after the highest-ranking females (rank 1), and were first observed to mate 4.3 ± 0.4 days after the rank 1 females.

There was some evidence that females actively sought copulations with nonguarding males. On days when they were being guarded, females accepted a lower proportion of their guarding male's mounting attempts than those of nonguarding males (mate-guarding males: mounting attempts/h=2.63 (IQR=0.88), percentage accepted=35 (IQR=22.8); nonguarding males: mounting attempts/h=1.07 (IQR=1.14), percentage attempts accepted=60 (IQR=42.8); Wilcoxon signed-ranks test of percentage attempts accepted: $T^{+}=59$, $N=11$, $P<0.05$). The strongest evidence that females tried to escape attempts by males to control their mating behaviour, however, came from anecdotal observations: if a mate-guarding male became separated from his female (for example, because he stopped to eat a beetle), his female often ran away from the pack and mated with another male out of sight of the guarding male. Out of 24 females in oestrus, 11 were observed to mate with a single male, seven mated with two males, three mated with three males and one was observed to mate with five males in a single oestrus.

Male Mating and Mate-guarding Behaviour

A mean of 26 ± 3.4% of adult male pack members guarded females during pack oestrus ($N=7$ packs). Mate-guarding males typically followed a female throughout the morning and afternoon foraging trips, maintaining close proximity to her. In 26 10-min focal watches on seven guarded females, mate-guarding males were the closest individuals to guarded females on 78 ± 5.0% of time intervals, and the mean distance between the female and her mate guard over the focal period was 1.2 ± 0.2 m. Guarding males guarded a mean of 1.7 ± 0.1 females per oestrus (range 1–3). In seven packs, mate-guarding males were heavier and larger than adult males in the same pack who did not guard (paired t test: weight: $t_6=2.7$, $P<0.05$; head–body length: $t_6=2.52$, $P<0.05$; head width: $t_6=2.754$, $P<0.05$). There was a tendency for mate-guarding males to be older than nonguarding packmates (Wilcoxon signed-ranks test: $T^{+}=24$, $N=7$ packs, $P=0.11$), and to have larger testes (paired t test: $t_6=2.23$, $P=0.067$), although not significantly so.

Mate-guarding males were highly aggressive to any males who approached the female they were guarding. Aggressive acts usually took the form of snaps, lunges and pounces on other males. The rate at which mate-guarding males were aggressive to other males was 6.7 times greater than the equivalent rate at which these same males were aggressive towards other males in nonoestrous periods (aggressive acts/h: oestrus=3.1 (IQR=1.6), non-oestrus=0.46 (IQR=0.81); Wilcoxon signed-ranks test: $T^{+}=28$, $N=7$, $P<0.05$). By contrast, rates of female–female aggression during oestrous and nonoestrous periods were not significantly different (aggressive acts/h: oestrous=0 (IQR=0.32), nonoestrous=0.73 (IQR=1); Wilcoxon signed-ranks test: $T^{+}=18$, $N=7$, NS). Commonly, a mate guard and his female were shadowed by one or two 'sneaky' males waiting for an opportunity to mount the female, and these individuals were the target of most of the aggression by guarding males. The victims of aggression occasionally retaliated, leading to short fights which included scratching and biting by both parties, but invariably the guarding male succeeded in displacing its opponent.

The mating attempts of nonguarding males were more likely to be interrupted by other males within the first 20 s than those of mate-guarding males (percentage of interruptions: mate-guarding males=54% (55/102); nonguarding males=72.6% (77/106); G test: $G_1=3.47$, $P<0.1$), although not significantly so. Across six packs, a median of 83.7% (IQR=25) of all observed matings involved a mate-guarding male. Per male, mate-guarding individuals obtained a median of 31.1% (IQR=21) of the observed matings in each pack, whereas the corresponding figure per nonguarding male was 1.8% (IQR=3.3; Wilcoxon signed-ranks test: $T^{+}=21$, $N=6$, $P<0.05$). There was a high

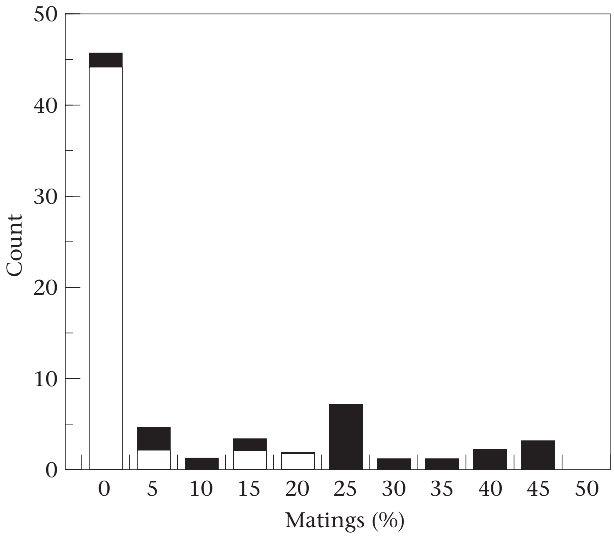

Figure 2. Distribution of observed matings among male members of one habituated pack. Data shown are pooled from six oestrous periods. A single 'count' is one male in one oestrous period. ■: Males who mate guarded; □: nonguarding males.

degree of skew in the distribution of matings among male pack members, with a few mate-guarding males monopolizing the majority of the observed matings and the majority of males apparently failing to mate at all during oestrus (Fig. 2).

However, it is likely that the distribution of observed matings underestimates the true number of matings obtained by nonguarding males. Matings with nonguarding males were more surreptitious than matings with guarding males, and are likely to have been more difficult to detect. Ninety-two per cent (12/13) of matings with nonguarding males took place out of sight of other adult males in the pack compared to 64% (16/25) of matings with guarding males (*G* test: $G_1=4.08$, $P<0.05$). In many cases, nonguarding males and females disappeared into a bush together, but it was impossible to confirm whether mating had occurred.

Patterns of Pregnancy

The mean proportion of adult females found to be pregnant when trapped 2–6 weeks after a pack oestrus was 0.83 ± 0.05; $N=60$ females). From observational data, however, the proportion that were visibly pregnant in the later stages of gestation (6–8 weeks) was 0.71 ± 0.05 ($N=12$ packs), suggesting that females may commonly abort or resorb fetuses before pregnancy becomes visible. Of 32 breeding attempts in 12 packs, five involved one visibly pregnant female, four involved two pregnant females, eight involved three females, six involved four females, four involved five females, three involved six females and two involved seven females.

There was no significant effect of rainfall during the month of oestrus, nor during the month in which females gave birth, on the proportion of females in the pack becoming pregnant (generalized linear regression: $N=32$ breeding attempts in 12 packs; rainfall during oestrus: $F_{1,30}=0.43$, NS; rainfall at birth: $F_{1,30}=0.02$, NS). However, there was a significant effect of pack in this analysis ($F_{11,30}=23.01$, $P<0.05$).

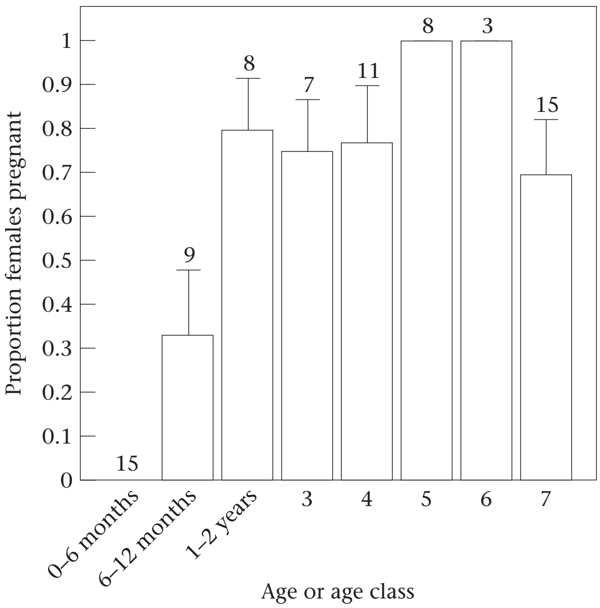

Figure 3. Proportion of pack females getting pregnant as a function of age or age class. Data are from 19 breeding attempts in 10 packs. Means are shown+SE. Numbers above columns indicate number of breeding attempts that included females of that age class.

The youngest females to conceive did so at the age of 290 days. When females were trapped after pack oestrus, one-third (32.8%) of females under 12 months of age were found to be pregnant. There was no significant difference in residual weight between females who became pregnant before the age of 12 months and their female littermates who did not (subadults who became pregnant, $N=6$, percentage residual weight$=-1.31$; other females from same litter, $N=9$, percentage residual weight$=-0.28$; Mann–Whitney: $U'=29$, NS).

Among adult females, there was no significant difference between age classes in the proportion becoming pregnant (as determined by trapping; ANOVA: $F_{5,50}=0.89$, NS; Fig. 3). The average body condition of adult females who got pregnant during a breeding attempt was higher than the average body condition of those adult females in the same pack who failed to get pregnant in the same breeding attempt (pregnant females' body condition$=1.03 \pm 0.19$; nonpregnant$=0.95 \pm 0.04$; paired *t* test: $t_{10}=2.28$, $P<0.05$). However, in three of these breeding attempts, the only female not to get pregnant was clearly sick and emaciated. When these three sick females were excluded from the data, there was no significant difference between the condition of females who did and did not get pregnant (pregnant females$=1.03 \pm 0.19$; nonpregnant$=0.99 \pm 0.03$; paired *t* test: $t_7=1.25$, NS).

The mean number of fetuses per female was 2.84 ± 0.12 ($N=50$). There was a nonsignificant tendency for mean fetal litter size to increase with age class (Spearman rank correlation: $r_s=0.24$, $N=50$, $P=0.09$; Fig. 4a). However, the oldest age class (class 7) included some females with

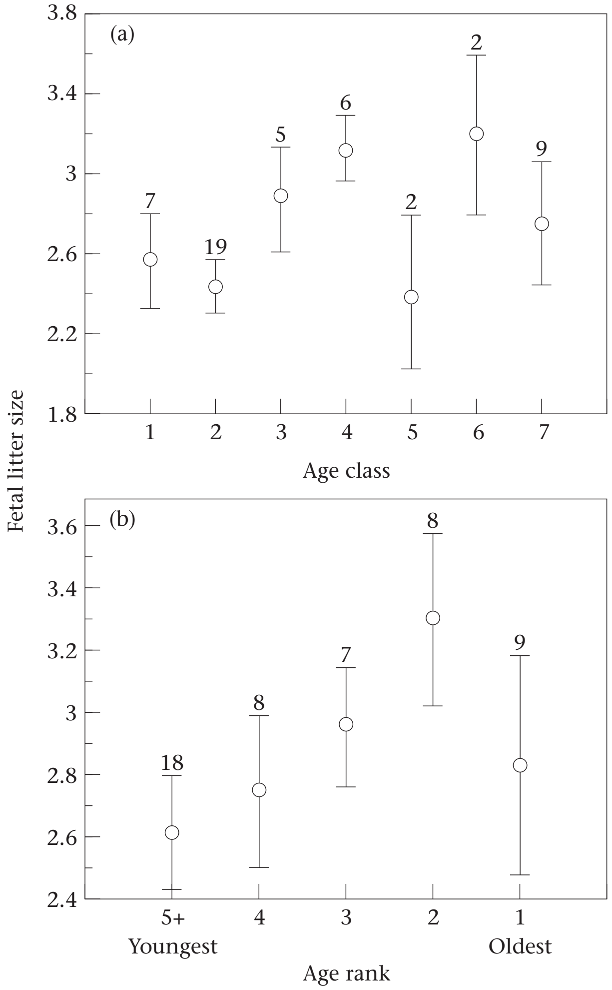

Figure 4. (a) Fetal litter size against age class of mother. (b) Fetal litter size against mother's age rank in the pack. Data are pooled from 50 females in 10 packs. Means are shown±SE. Numbers indicate number of pregnant females in each age class or rank.

extremely worn teeth who were in poor condition. When these oldest females were excluded (i.e. excluding class 7), there was a significant increase in mean fetal litter size with age class (Spearman rank correlation: $r_s=0.34$, $N=41$, $P<0.05$). Similarly, across all age ranks, there was no consistent relationship between fetal litter size and age rank in the pack (Spearman rank correlation: $r_s=0.196$, $N=50$, NS; Fig. 4b), but when the oldest females in each pack were excluded, there was a significant correlation between age rank and fetal litter size (Spearman rank correlation: $r_s=0.328$, $N=41$, $P<0.05$), with older-ranking females carrying more fetuses.

Synchrony of Parturition and Length of Gestation

On nine (82%) of 11 occasions for which multiple females in a pack were pregnant and the exact day of parturition was known for each pregnant female, all the females gave birth on the same day. From three to seven females gave birth synchronously in this way. On the two occasions where parturition was known to be asynchronous (i.e. females gave birth on different days), females gave birth 2 days apart. In one case, the eldest of five pregnant females gave birth 2 days before the others gave birth together; on the other occasion the two eldest of four pregnant females gave birth on one day, and 2 days later the other two gave birth together. Both asynchronous litters failed before emergence, while the failure rate for synchronous litters was two out of nine (*G* test: $G_1=2.09$, NS).

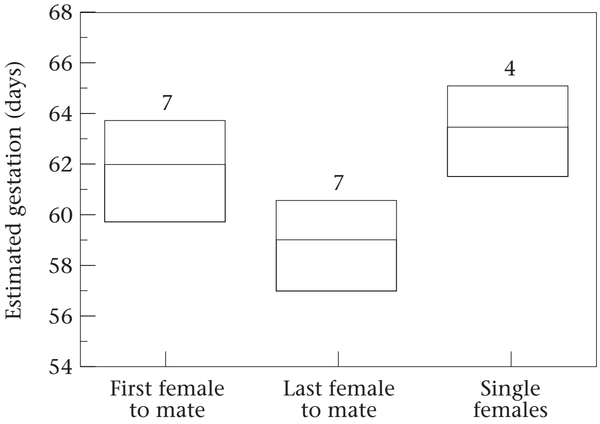

Figure 5. Estimated gestation period of first-mating and last-mating females in breeding attempts with multiple breeding females, and that of females in breeding attempts involving only one breeding female ('single females'). Boxes show medians and interquartile ranges. Numbers indicate number of breeding attempts.

In breeding attempts involving several females, the estimated gestation period of the first female (or females) to mate averaged 62 days (IQR=4.0), which was not significantly different from the estimated gestation period in packs in which there was only one breeding female (63 days (IQR=3.5); Mann–Whitney *U* test: breeding attempts involving more than one female, $N=7$; breeding attempts involving one female only, $N=4$; $U=19$, NS). However, in breeding attempts involving several females, the estimated gestation period of the last females to mate was 59 days (IQR=3.5) which was significantly shorter than that of single females (Mann–Whitney *U* test: $U=26$, $N_1=7$, $N_2=4$, $P<0.05$; Fig. 5).

Survivorship of Pups

Sixteen (50%) of 32 litters failed before any pups emerged from the den. In most cases the cause of failure was unknown. In three cases, litters failed immediately after a neighbouring pack attacked the natal den. Direct evidence of extragroup infanticide came on a fourth occasion when a dominant male was seen to enter the breeding den of a rival pack, drag out a live pup, and kill it.

Interbirth interval after a failed breeding attempt was not significantly different from that after a breeding attempt in which some pups emerged from the den (Mann–Whitney *U* test: $U=22.5$, $N_1=N_2=6$, NS). Among those litters that emerged, the average number of pups

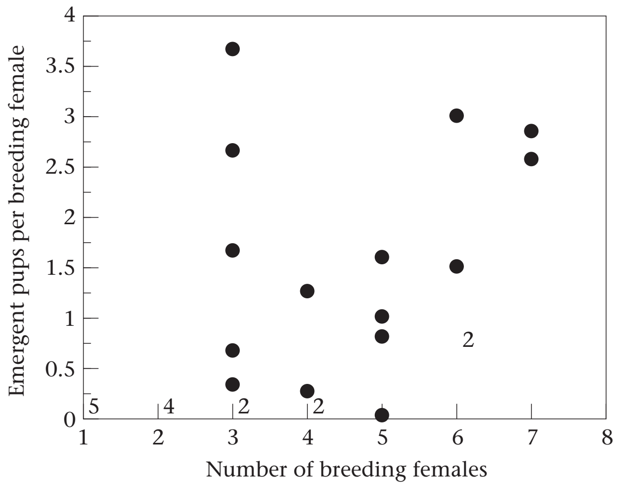

Figure 6. Number of pups emerging per breeding female against number of breeding females. Data are from 30 litters in 10 packs. See Table 2 for results of generalized linear regression.

emerging was 7.8 ± 1.51 (N=16 litters). Pups remained in the den for an average of 25 days (range 23–27, N=6 litters) before they started to be escorted on short afternoon foraging trips with the rest of the pack. Within 1 week of emergence from the den, pups began to accompany adults on morning as well as afternoon foraging trips.

In a generalized linear regression the number of pups emerging per breeding female increased with the number of breeding females ($F_{1,28}$=18.32, P<0.001; Fig. 6). All other terms in the model had no significant effect (Table 2). Five breeding attempts that involved a single breeding female, and four that involved two breeding females, all failed before emergence. When these nine breeding attempts were excluded from the data, the relationship between number of emergent pups per breeding female and number of breeders bordered on significance ($F_{1,19}$=4.2, P=0.059).

A mean of 56.2 ± 8.5% of emergent pups survived to 3 months after emergence (N=16 emergent litters). There was no correlation betweeen litter size at emergence and survivorship to 3 months postemergence (N=16 emergent litters, r^2=0.007, $F_{1,14}$=0.111, NS). Nor was there any correlation between postemergent survivorship to 3 months and pack size, number of males, or number of females (excluding individuals under 6 months old; simple multiple regression: N=16 litters, r^2=0.026, $F_{3,12}$=1.135, NS; partial regression coefficients (c_i) and associated t values: $c_{\text{pack size}} = -0.055$, $t_{12} = -1.822$, NS; c_{males}=0.053, t_{12}=1.512, NS; c_{females}=0.046, t_{12}=0.646, NS).

Within-group Infanticide

There was good evidence of two within-group infanticides during this study. Both were apparently carried out by males. In February 1997, four females gave birth over a period of 2 days (i.e. the litter was asynchronous). Five days later, a subadult male (aged 9 months) emerged from the breeding den carrying a pup in his mouth and ran into some adjacent thickets, closely followed by a number of adult males and females calling loudly. Over a period of a few minutes, all of the animals, including the subadult male, re-emerged from the bush and returned to the breeding den. The pup was not brought back, and was not seen again. Two hours later the pack moved away from the den site. Only one pup from this litter survived to emergence from the den, 2 weeks later.

The second presumed infanticide occurred in very similar circumstances. In March 1997 three females gave birth synchronously. Four days later a dominant male (aged over 4 years) was seen to carry a live, screaming, pup out of the breeding den and run into a nearby thicket. Again, a large number of his packmates pursued him, twittering excitedly, and again all these individuals eventually returned to the den, without the pup. No pups emerged from this litter. Unfortunately, in both these cases of suspected infanticide it was not possible to search for more direct evidence that the pups had been killed because of the thickness of the surrounding vegetation.

Table 2. Results of general linear regression of number of emergent pups per breeding female

Term in the model	Estimate (SE)	*df*	*F* ratio	*P*
Number of breeding females	0.078 (0.018)	1	18.32	<0.001
Terms not in the model				
Pack size	—	1	2.96	0.096
No. nonbreeding females	—	1	1.20	NS
No. males	—	1	0.22	NS
Provisioned or unprovisioned	—	1	0.34	NS
Pack	—	9	0.45	NS

Data are from 30 breeding attempts in 10 packs. The response variate, number of emergent pups per pregnant female, was first transformed using log(Y+1) to avoid problems with zeros in the data and to allow the specification of a normal error structure.

DISCUSSION

Control Over Mating Opportunities

The majority of the males in banded mongoose packs are prevented from mating with oestrous females by socially dominant, mate-guarding males. (Hereafter I use 'dominant' and 'subordinate' to refer to mate-guarding and nonguarding males, respectively.) Dominant males guarded females closely through the period for which they were most receptive, and were highly aggressive to any other males who came too close to their guarded female. Although only 26% of males in a pack engaged in mate-guarding behaviour, these males obtained the great majority of observed matings. However, I probably underestimated the number of matings by subordinate males, since these matings were more surreptitious than matings with dominants, and many matings may have taken place out of sight of observers. Moreover, guarded females behaved in such a way as to facilitate matings with multiple males; for example, they attempted to escape from their mate guard where possible, and refused a greater proportion of their guard's mounting attempts than those of nonguarding males. Even though matings with subordinate males were difficult to detect, the results indicate that attempts to monopolize access to oestrous females often fail: almost half of the females in this study were observed to mate with more than one male in a single oestrus.

Since females are sometimes able to escape their mate guard to mate with subordinates, these results show that control of the distribution of copulations among males is shared between dominant males and breeding females. Clearly, females prefer a more even distribution of reproduction among males than dominant males, perhaps because this maximizes the amount of paternal investment their offspring receive (as in dunnocks, *Prunella modularis*: Davies 1992; Houston et al. 1997). Thus, among male banded mongooses, as in many other cooperative breeders that live in mixed-sex groups, the central assumption of concession models of reproductive skew, namely, that a single dominant has full control over reproduction, is violated. The final distribution of paternity will reflect the relative ability of males and females to enforce their particular optimal degree of skew. Although the conflict of interest between males and females has been the focus of theoretical work concerning the link between paternity and paternal care (e.g. Houston et al. 1997), reproductive skew models have yet to incorporate the possibility of female control over skew among males. Such extensions to skew theory are necessary if we are to understand the evolution of skew among males living in mixed-sex groups.

In stark contrast to the pattern among males, banded mongoose females made no effort to interfere with each other's mating attempts, and there was no increase in female–female aggression during oestrus. Nevertheless, a striking pattern emerged in the order of mating among females, with the oldest females in each pack being mate guarded and mated before younger females. Since it is typical for all the pregnant females in a pack to give birth on the same day, older females apparently have a longer gestation than their younger packmates. This interpretation is strengthened by the finding that, in breeding attempts involving several females, the gestation period of first-mating females was 'normal' (in the sense that it was no different from that of females who were the sole breeders in a pack), whereas the gestation period of last-mating females was significantly shorter than this norm. Younger females tended to carry fewer fetuses than their older packmates, raising the interesting possibility that they might compensate for reduced development time in utero by producing fewer young.

Why Do Some Females Mate Before Others?

One of the consequences of the staggered pattern in which females mated was that it enabled the same few males who guarded the oldest pack females to move on to guard the youngest. Thus, one argument would be that delayed oestrus in young females has evolved for this reason. By delaying mating, young females may obtain genetic benefits from mating with the largest, most dominant males (a variation of the 'best-male' hypothesis; Clutton-Brock & Harvey 1976; Hrdy & Whitten 1987), or perhaps obtain insurance against infanticide by dominant males. However, the finding that females attempted to mate with males other than their mate guard (and were usually successful) suggests that any such advantage associated with fertilization by guarding males is likely to be small.

An alternative explanation is that the observed disparity in oestrus reflects the latency with which some females in the group can respond to behavioural and/or pheromonal cues signalling the onset of oestrus. One or more dominant females may act as a reproductive 'zeitgeber', with whom other females in the pack attempt to synchronize ovulation and fertilization. Where subordinates are forced to give birth on the same day as dominants to avoid infanticide (see below), this would serve to minimize the costs of reduced gestation. Whether or not banded mongooses are induced ovulators (as is suspected for dwarf mongooses, *Helogale parvula*; Creel et al. 1992), the increase in oestrogen associated with behavioural oestrus may take some time to effect (Nelson 1995), with the result that subordinate females may be constrained to enter oestrus a few days after dominants. This hypothesis could be tested by removing the oldest females to captivity on the first day of oestrus and replacing them a few days later. One would predict that, in the absence of the oldest females, oestrus in younger females would be inhibited or delayed.

Reproductive Skew and Suppression in Banded Mongooses

The results indicate little or no reproductive suppression in banded mongoose females, at least prior to parturition. There was no evidence of delayed sexual maturation or inhibition of receptivity, since females were sexually receptive from the age of 12 months, and almost all adult females were observed to mate. Around 83% of adult females conceived during oestrus, and around 71% carried to term and gave birth together. The only females that failed to reproduce were ill or in very poor condition. There was no effect of rainfall around the time of mating or birth on the proportion of females becoming pregnant in each breeding attempt. These observations stand in marked contrast to the patterns seen in other social mongooses where usually only a single female breeds. For example, the proportion of breeding attempts in which more than one female is pregnant is 20% for suricates, *Suricata suricatta* (Clutton-Brock et al. 1999; T. Clutton-Brock, personal communication) and 27% for dwarf mongooses (Rood 1980, 1990; Creel & Waser 1991, 1997; see also Rasa et al. 1992 for information on yellow mongooses, *Cynictis penicillata*), whereas in the current study the figure was 84%. Why do such a high proportion of females reproduce in banded mongooses? All models of reproductive skew, whether they are based on reproductive concessions or limited control, assume that a dominant individual suffers reduced direct fitness when a subordinate reproduces. However, my finding that per capita survivorship of banded mongoose pups increased with the number of females that had given birth suggests that this may not always be the case. Assuming that her young survive at least as well as those of other females, a dominant banded mongoose female would stand to gain nothing by attempting to suppress reproduction in her subordinates.

Why the per capita reproductive output of females should increase with the number of breeding females remains unclear, but there are three main possibilities: (1) survivorship may be causally related to the number of pups, that is, there may be litter size effects; (2) survivorship may be causally related to the number (and identity) of breeders; (3) both survivorship and the number of breeders are related to some third factor, such as territory quality. The result that pack identity and access to supplementary food had no significant effect on survivorship weighs against this last hypothesis and I do not consider it further. The first two possibilities are discussed below.

First, why might individual pups survive better in larger litters? One explanation is that predation or infanticide by the members of neighbouring packs may be a greater threat to pup survival than within-litter competition for resources. In such circumstances, a predator dilution effect in large litters may outweigh the costs of increased competition for food in larger communal litters, so that per capita survivorship increases with litter size, at least up to a point (Lack 1947; Pulliam & Caraco 1984). In a recent skew model, Cant & Johnstone (1999) showed that where total productivity increases with litter size, dominant females may maximize their inclusive fitness by sharing reproduction with close relatives (the ‘beneficial sharing’ effect). In the present context, this hypothesis predicts that the parentage of surviving pups will be distributed among the most closely related females in the pack.

The second possibility is that pup survival depends on the number and/or identity of females, rather than on litter size per se. In particular, within-group infanticide by males or females could be responsible for the observed patterns of survival and reproduction. The only two within-group infanticides witnessed in this study were both carried out by males, suggesting that infanticide by male packmates does pose a real threat to the reproductive success of females. In breeding attempts involving many breeding females, matings (and paternity) may be shared among a larger proportion of male pack members, reducing any incentive they may have to commit infanticide (Smuts 1986; Creel & Waser 1997). Similarly, some females in a banded mongoose pack may commit infanticide if they have not contributed to the communal litter. Although female infanticide was not observed in this study, in captive banded mongooses it is a common occurrence (C. Fountain, personal communication). In dwarf mongooses and suricates, both breeding and non-breeding females have been observed to kill the young of other females in the group (Rasa 1973, 1994; Rood 1980; Clutton-Brock et al. 1998; S. Creel, personal communication). If within-group infanticide is responsible for the observed patterns of survival, one would expect that the parentage of successful litters will be shared among distantly related individuals, since unrelated males and females are most likely to commit infanticide (Johnstone & Cant 1999b; but see Clutton-Brock et al. 1998). Microsatellite analysis is currently underway to analyse the parentage of surviving young, and thereby cast light on both the true degree of reproductive skew, and the possible reasons for litter failure.

Birth Synchrony and Infanticide

Whatever the reason why individual pups survive better when more females give birth, one would expect that at some point the costs of increased competition for food will outweigh any benefits derived from reduced predation or infanticide. It is likely, therefore, that dominant females will benefit from allowing some, but not all, the females in a group to reproduce. Infanticide may represent the chief weapon by which females attempt to prevent unsanctioned reproduction, but the power of this weapon will be limited by their ability to discriminate which offspring belong to which female (Johnstone & Cant 1999b). This task will prove particularly difficult when a number of subordinate females synchronize reproduction to the same day as the dominant. In these circumstances females who commit infanticide may run the risk of destroying their own offspring (Hrdy & Hausfater 1984; but see Creel & Waser 1997). Similarly, synchronous birth removes the only clue males may have as to whether they could have fathered some of the litter, namely, whether they mated with any of the mothers.

If such tight birth synchrony has evolved as a means of evading control by infanticidal males or females, one would expect there to be some considerable disadvantage to giving birth on different days. By contrast, if the main cause of pup mortality in the den was predation, attacks by neighbouring packs, or competition for resources, one would predict little or no difference in failure rate between breeding attempts in which all females gave birth on the same day and those in which females gave birth 2 or 3 days apart. More data on asynchronous litters are required to test this prediction.

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