

Female eviction, abortion, and infanticide in banded mongooses (*Mungos mungo*): implications for social control of reproduction and synchronized parturition

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Most cooperatively breeding species exhibit high reproductive skew, where reproduction within the social group is monopolized by a dominant pair. In many of these species, social control of reproduction is the mechanism driving reproductive skew: individuals within the social group actively reduce the reproductive success of others. In species where females do not suppress conception in other females, alternative routes to skewing the social group's reproductive output include inducing abortion in rivals, evicting them, or killing their young. This study examines instances of female eviction, abortion, and infanticide in a cooperatively breeding species with low preparturition reproductive skew, the banded mongoose (*Mungos mungo*). Although instances of these behaviors are rare in this species, aspects of their occurrence have implications for social control of reproduction. Abortion can be induced by the stress of being evicted. The readmittance of females that abort suggests that reducing communal litter size is a possible selective pressure for eviction. This is supported by the occurrence of eviction events in groups with relatively high numbers of reproductive females and by the eviction of young reproductive females. The timing of abortion events suggests that synchronization of parturition with other females in the group is a major selective pressure. Infanticide could represent the selective pressure for synchronized parturition. Alternatively, synchronization may minimize competitive asymmetry between pups born to different females. This paper also describes incidences where a female aborts or gives birth to her litter over different days in order to synchronize parturition: behavior previously unrecorded in mammals. *Key words*: abortion, communal breeding, cooperative breeding, eviction, infanticide, reproductive skew, synchrony. [*Behav Ecol* 17:664–669 (2006)]

The factors that affect fecundity and reproductive success in social species are of particular interest due to the possible influence of social control. In the majority of cooperatively breeding species, where individuals help to rear young that are not their own offspring, breeding is usually monopolized by a single dominant pair that prevent subordinates from breeding (Stacey and Koenig 1990; Solomon and French 1997). Preparturition social suppression of subordinate reproduction by dominant individuals can include active behavioral harassment or apparently passive suppression (lacking aggressive behavior) of hormone levels (Reyer 1986; Creel et al. 1992; Johnstone and Cant 1999a, 1999b; Faulkes and Bennett 2001). Behavioral and endocrine mechanisms that prevent or terminate pregnancy (avoiding or reducing gestation costs) likely represent derived mechanisms that evolve in response to the selection pressures established by ancestral postparturition modes of suppression.

Mechanisms of postconception suppression, for example, eviction, stress-induced abortion, and infanticide are apparent in numerous social species. Postconception suppression is most obvious in cooperative breeding species with high reproductive skew, particularly when preconception reproductive suppression has apparently failed. For example, eviction, stress-induced abortion, and infanticide are used to skew reproductive success by dominant females in meerkats (*Suricata*

suricata) when the dominant has failed to suppress subordinate conception (Clutton-Brock et al. 1998, 2001). Eviction, abortion, and infanticide also occur in dwarf mongooses (*Helogale parvula*), African wild dogs (*Lycaon pictus*), and Arabian babblers (*Turdoides squamiceps*) (Zahavi 1990; Rasa 1994; Creel and Waser 1997; Creel et al. 1997).

Where mechanisms of dominant controlled postpartum suppression persist, subordinate strategies to evade suppression are also likely to evolve. Voluntary dispersal is one method of evading suppression. Another method by which subordinate females could minimize infanticide of their young is to give birth in synchrony with the dominant female. A subordinate giving birth at the same time as a dominant may mask the temporal cues that a dominant could use to differentiate between her own and other's offspring (Manning et al. 1995). In social groups, parturition is commonly temporally clustered (Ims 1990).

This study concerns the banded mongoose, a group-living, cooperatively breeding species where up to 10 females can give birth together at the same time in the same den (Cant 2000; Gilchrist et al. 2004). The degree of synchrony of parturition is an important factor affecting the success of banded mongoose litters: with asynchronous litters exhibiting reduced reproductive success (Cant 2000; Gilchrist, forthcoming). There is no evidence for preconception social control in this species (most females conceive: Cant 2000; De Luca and Ginsberg 2001; Gilchrist et al. 2004). If the distribution of reproduction within banded mongooses is truly egalitarian, postconception reproductive conflict should exhibit similarly low reproductive skew. In this paper, I examine the frequency and circumstances of female eviction, abortion, and infanticide and consider whether instances of these behaviors follow

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patterns consistent with reproductive skew theory (e.g., Vehrencamp 1983; Keller and Reeve 1994; Clutton-Brock 1998; Reeve et al. 1998): that they occur when female reproductive competition is likely to be highest and that subordinate females are most vulnerable. Finally, I consider the evidence for infanticide, whether it could function as a mode of post-parturition reproductive suppression, and its implications for parturition synchrony within groups.

METHODS

Banded mongooses are small (<2 kg) insectivorous group-living mammals that live in equatorial Africa. Within groups, females come into behavioral estrus, and therefore also give birth (in the same den), approximately synchronously (Cant 2000). On average, a female breeds 3.79 ± 0.14 ($n = 56$ females) times a year.

Fieldwork was carried out in an 8-km² area around Mweya peninsula, Queen Elizabeth National Park, southwest Uganda 0°12'S and 27°54'E, from March 1997 to February 2000. Individuals were classified as adults (aged 365 days or more), subadults (183–364 days), infants (91–182 days), or pups (0–90 days). Females were classed as nonreproductive until their first conception. Group size included all individuals except pups. Data were collected on 464 individuals in 15 groups. Three groups had access to supplemental food at garbage dumps (groups 1b, 1d, and 2; Gilchrist and O'tali 2002; O'tali and Gilchrist 2004).

Individuals were regularly trapped and marked (for methods, see Cant 2000), and groups observed usually once per day. Procedures were licensed by the Uganda National Council for Science and Technology and the Uganda Wildlife Authority and followed the guidelines of the Association for the Study of Animal Behavior (ASAB 1991).

Eviction events were defined as incidences where one or more individuals were forcibly ejected from their group by other group members (Cant et al. 2001; Gilchrist 2001). Eviction events involved intense intrasexual aggression targeted at individual group members, differing dramatically from background aggressive interactions (Cant et al. 2001; Gilchrist 2001). Although males are also occasionally evicted (Cant et al. 2001; Gilchrist 2001), in this paper, I restrict consideration to female eviction events. All females targeted during eviction events resisted eviction and attempted to remain in and/or return to the group.

A communal litter was defined as a within-group parturition event including all females that gave birth within 30 days of one another (in reality, females often gave birth on the same day and rarely gave birth more than 5 days out of synchrony). By trapping and anesthetizing females 2–4 weeks after estrus (gestation is approximately 8 weeks; Cant 2000), it was possible to detect pregnancy and count the number of fetuses by gentle palpation. There is no evidence that trapping and palpating pregnant females affected the probability that they aborted ($\chi^2 = 2.37$, $df = 1$, $P = 0.13$, $n = 264$; 4 of 107 non-palpated females aborted and 14 of 157 palpated females aborted). For females that were not trapped, pregnancy was evident from the fourth week of gestation as females had a visibly swollen abdomen. Parturition or abortion was detected when the abdomen size returned to normal.

In order to minimize stress, pregnant females were rarely retrapped. Abortion was assumed to have occurred where a female that was confirmed as pregnant either by trapping or visual observation was not visibly pregnant when the group gave birth to the litter. In addition, when a female gave birth twice within 30 days, the first parturition was classed as an abortion. According to these criteria, abortion could include

fetal absorption and miscarriage. In most cases of abortion, females that aborted had been classified as visibly pregnant prior to abortion. Possible "invisible pregnancies" occurred where females that were identified as pregnant by trapping subsequently failed to show visible signs of pregnancy. These females could conceivably have gestated and given birth without detection. However, this is unlikely because all except one pregnant female that failed to show visible signs of pregnancy had 3 fetuses (the median fetus count; Gilchrist et al. 2004) counted at palpation (Table 2), and therefore, late pregnancy would have been visible.

If a female conceived and aborted prior to trapping and early in the gestation period (before 3 weeks gestation), then she could have been misclassified as a nonconception rather than as an abortion (within breeding attempts, 62 of 302 parous females were classified as nonconceptions). This is unavoidable and common to the majority of field studies considering conception frequency. However, it means abortion may have been underestimated.

Mongoose fecal samples were collected and analyzed for pup remains from the date one or more females in a group gave birth until the litter emerged and pups traveled with the group (approximately 27 days; Gilchrist 2001) or the litter failed and no pups emerged. Fresh fecal samples from identified individuals were individually collected, bagged, and labeled, and each sample was subsequently inspected using tweezers. The presence of mongoose pup claws in fecal samples is the only definitive sign that an individual had eaten a pup: mongoose claws are highly distinctive due to their structure and curvature. Of the 2400 fecal samples inspected, 1092 (from 6 groups) were collected within 2 days of parturition: the only period with infanticide recorded for meerkats (Clutton-Brock et al. 1998, 2001) and with pup remains found in fecal samples of the banded mongoose (Gilchrist 2001). If infanticide occurred in the subterranean den and the pups were not eaten, then infanticide would remain undetected. However, infanticide is commonly associated with cannibalism, notably in the other social mongooses, the meerkat and dwarf mongoose (Rasa 1994; Clutton-Brock et al. 1998).

Statistical analyses used GenStat 6 with the exception of the G-test for goodness of fit, used to test whether pregnant females that aborted were more likely to be reaccepted by the group (Sokal and Rohlf 1995). Where data sets allowed, I used mixed model statistical procedures to fit random terms and therefore account for repeated sampling across error terms (Schall 1991). Analysis of eviction events during group estrus used a generalized linear model (GLM). Eviction event (no eviction event = 0, eviction event = 1) was fitted as the dependent variable with binomial error distribution and logit link function. It was not possible to fit group as a random term to this model. Each fixed effect was fitted alone. Analysis of female age used a restricted estimate maximum likelihood model (REML) with female age (days) as the dependent variable and female eviction status (not evicted = 0, evicted = 1) as the fixed effect. Litter was fitted as a random term. The significance level was $P < 0.05$. All means are expressed as ± 1 standard error.

RESULTS

Eviction

During the study, 21 females were evicted in 4 eviction events (Table 1). These eviction events occurred during group estrus (eviction occurring during 4 of 67 group estrus events). In 3 of these eviction events (litters 1, 3, and 14 in Table 1), at least one of the females was permanently evicted, and in the other

Table 1
Summary of female eviction events in banded mongooses
(Mungos mungo)

Litter	Group	Female ID	Pregnancy status		Permanently evicted?
			Before eviction	After eviction/reacceptance	
1	1b	9b	Pregnant	Not pregnant ^a	No
1	1b	b7	Pregnant	Pregnant	Yes
1	1b	c8	Pregnant	Pregnant	Yes
1	1b	m2	Pregnant	Pregnant	Yes
1	1b	m3	Pregnant	Pregnant	Yes
1	1b	m4	Pregnant	Pregnant	Yes
2	1b	r4	Not pregnant	Not pregnant	No
2	1b	s2	Pregnant	Not pregnant ^a	No
2	1b	s3	Pregnant	Not pregnant ^a	No
2	1b	t1	Pregnant	Not pregnant ^a	No
2	1b	t5	Pregnant	Not pregnant ^a	No
3	2	45	Pregnant	Not pregnant ^a	No
3	2	59	uk	Not pregnant	No
3	2	1p	uk	uk	Yes
3	2	1q	uk	uk	Yes
3	2	8k	uk	Not pregnant	No
3	2	9j	uk	Not pregnant	No
14	1b	5q	uk	uk	Yes
14	1b	5s	uk	uk	Yes
14	1b	8g	uk	uk	Yes
14	1b	8i	uk	uk	Yes

uk, unknown.

^a Confirmed to have aborted during eviction.

eviction event (litter 2, Table 1), all females that were evicted managed to regain entry to their group. In these eviction events, all 6 of the females that aborted while they were being forcibly evicted from their group were accepted back into

their group, whereas pregnant females that were not reaccepted by their group (and whose posteviction pregnancy status was known) maintained pregnancy (*G*-test, $G = 13.3$, $df = 1$, $P = 0.0003$, treating females as independent units).

In litter 1 (Table 1), the single female that managed to regain acceptance had aborted, whereas all 5 females that were successfully evicted remained pregnant. In litter 2 (Table 1), 4 of the 5 evicted females were pregnant prior to eviction, and all 5 were not pregnant on regaining acceptance to the group. In litter 3 (Table 1), the only female known to be pregnant was not pregnant on regaining acceptance to the group (the other 3 females to regain acceptance were similarly not pregnant on reacceptance to the group, but their pregnancy status prior to eviction was not known). Finally, in litter 14 (Table 1), the pregnancy status of the 4 evicted females was unknown (before and after eviction).

The occurrence of eviction events was positively correlated with the number of reproductive females present at estrus (GLM: $\chi^2 = 12.82$, $df = 1$, $P < 0.001$; noneviction estrus = 4.75 ± 0.030 reproductive females, $n = 63$; eviction estrus = 9.25 ± 0.48 reproductive females, $n = 4$; Figure 1), which was a more highly significant positive correlate of eviction than group size ($\chi^2 = 7.39$, $df = 1$, $P = 0.007$). The occurrence of eviction was not significantly correlated with the number of adult and subadult females ($\chi^2 = 3.3$, $df = 1$, $P = 0.07$), the number of adult females ($\chi^2 = 1.8$, $df = 1$, $P = 0.18$), or the number of adult males ($\chi^2 = 0.35$, $df = 1$, $P = 0.55$). Reproductive females evicted during estrus were younger than reproductive females not evicted during estrus (REML: $\chi^2 = 24.23$, $df = 1$, $P < 0.001$, $n = 37$; nonevicted age = 1214.5 ± 186.0 days, $n = 17$; evicted age = 590 ± 182.8 days, $n = 20$; Figure 2). This result was consistent on including nonreproductive subadult females: females evicted during estrus were younger than females not evicted during estrus (REML: $\chi^2 = 7.93$, $df = 1$, $P = 0.005$, $n = 43$; nonevicted age = 1013.7 ± 129.5 days, $n = 21$; evicted age = 579.4 ± 126.5 days, $n = 22$).

Table 2
Instances of abortion in banded mongoose (*Mungos mungo*) groups

Litter	Group	Number of females gave birth	Female ID	Abortion circumstance ^a	Date group conception	Fetus count ^b	Day of abortion ^c
1	1b	4	9b	Eviction	23/05/1999	—	49
2	1b	4	t1	Eviction	06/10/1999	3	56
2	1b	4	s2	Eviction	06/10/1999	3	51
2	1b	4	t5	Eviction	06/10/1999	3	55
2	1b	4	s3	Eviction	06/10/1999	3	55
3	2	1	45	Eviction	22/07/1998	3	41
4	1b	0	9e	Unknown	16/02/1998	3	63 ^d
5	1b	6	c8	Unknown	07/10/1998	3	50
6	2	3	e7	Unknown	10/02/1999	—	42
7	2	6	8k	Unknown	20/04/1999	—	42
7	2	6	9j	Unknown	20/04/1999	—	42
8	1b	4	t5	IP	31/07/1999	3	—
9	1c	2	4m	IP	19/07/1998	3	—
10	2	0	h8	IP	11/06/1999	3	—
10	2	0	d6	IP	11/06/1999	2	—
11	5	3	100	IP	28/07/1997	3	—
12	11	2	q2	IP	25/07/1999	3	—
13	11	2	q2	IP	30/09/1999	3	—

Litter numbers correspond to Table 1.

^a Eviction: eviction events involved group members being forcibly ejected from their group by other group members (Cant et al. 2001).

IP: possible "invisible pregnancy," where female identified as pregnant by trapping subsequently failed to show visible signs of pregnancy.

^b Fetuses counted by palpation. —: not counted.

^c Counted from estimated date of conception. Gestation period ranges from 57 to 66 days (Cant 1998).

^d Female observed miscarrying fetus.

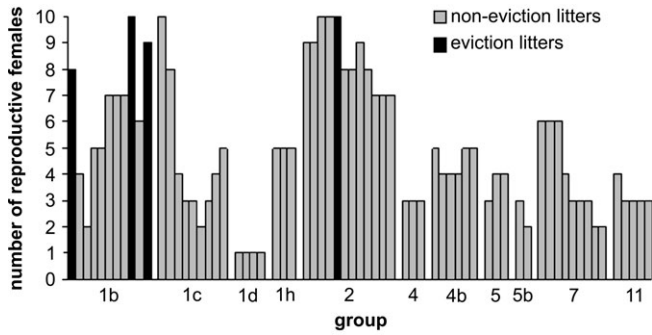


Figure 1
The number of reproductive females present for each estrus event in banded mongoose groups. The number of reproductive females was relatively high for estrus events where females were evicted. For each group, litters are plotted in chronological order. Group 1b eviction litters correspond to eviction litter numbers 1, 2, and 14 (Table 1). Group 2 eviction litter corresponds to eviction litter number 3 (Table 1).

Abortion

Abortion was rare. There were 18 abortions (within 6 of the 11 groups with abortion data distributed among 13 of 69 communal litters) and 246 successful gestations: an overall abortion rate of 6.8%. Details of the 18 abortions are given in Table 2. Six abortions occurred during eviction events (in 2 eviction events, a single female aborted, and in another eviction event, 4 females aborted). There was no obvious cause for the remaining 12 abortions: 5 occurred relatively late in the gestation period (distributed among 4 litters: 3 litters with a single abortion and one litter with 2 abortions), and 7 were possible invisible pregnancies (distributed among 6 litters: 5 litters had a single invisible pregnancy, and one litter had 2

invisible pregnancies). Only one abortion was observed, where the female was seen to miscarry one of her 3 fetuses (litter 4, Table 2).

Synchrony

Banded mongooses show a high degree of synchronization of parturition relative to other mammalian species. All females within a group gave birth on the same day in 11 of 38 litters where multiple females gave birth and the day of parturition was known for all females. The degree of synchronization in asynchronous litters was also impressive: median estimated duration between first and last sublitters was 5 days, interquartile range 3–13 days).

Some of the abortions with no known cause occurred on the same day that other females gave birth. On one occasion (litter 10, Table 2), of 2 females that were approximately 2 weeks pregnant when trapped (gestation estimated by palpation), one female became visibly pregnant and gave birth with 3 other females 67 days later (estimated gestation period 57–66 days; Cant 1998) and therefore either extended gestation or aborted early in order to conceive and give birth in synchrony with the other females. The second female was never visibly pregnant.

The following occurrences suggest that the females miscarried some but not all the fetuses they were gestating and then gestated the remaining fetuses to full term. On one occasion (litter 6, Table 2), a female that had been visibly pregnant aborted in synchrony with 3 pregnant females that gave birth. The female subsequently became visibly pregnant and gave birth in synchrony with the remaining 2 pregnant females 21 days later. In a similar occurrence (litter 7, Table 2), 2 visibly pregnant females aborted in synchrony with 6 females that gave birth, but both subsequently became visibly pregnant and gave birth in synchrony with other females 18 days later.

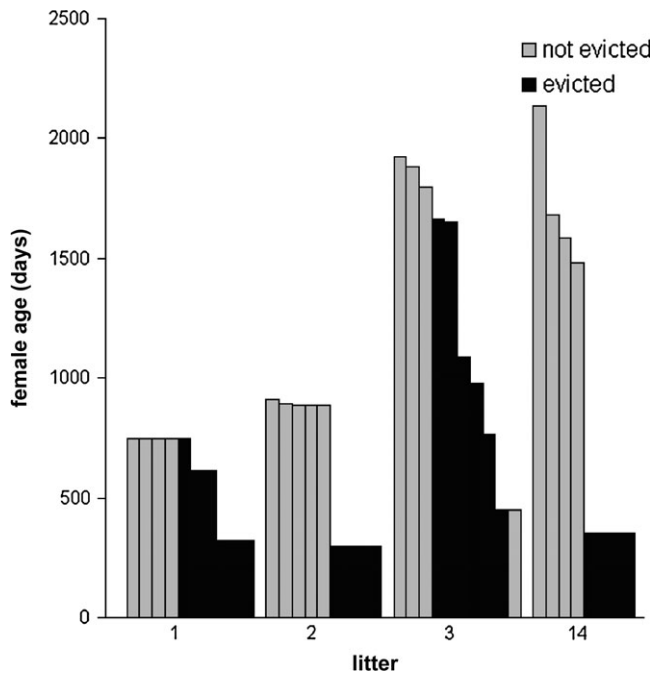


Figure 2
The age of reproductive females present in banded mongoose groups that underwent a female eviction event during estrus. The majority of evicted females were relatively young compared with females that were not evicted in the same litter. Litter numbers correspond to Table 1.

Infanticide

Infanticide is rare: only 4 fecal samples contained pup remains (of 2400 fecal samples inspected). In one litter, pup claws were found in the feces of 3 females. In the other litter, pup claws were found in the feces of the dominant male (Gilchrist 2001). Intragroup infanticide was never observed during behavioral observations.

DISCUSSION

Possible explanations for the absence of reproductive monopolization in species with low reproductive skew include a lack of costs to multiple female breeding, an inability to suppress reproduction in others, and costs of suppression exceeding the benefits. The banded mongoose is a communal breeding species with an egalitarian sharing of reproduction for the preparturition component of reproductive success (Cant 2000; De Luca and Ginsberg 2001; Gilchrist et al. 2004). Although there is evidence of reduced postparturition reproductive success with increasing numbers of breeding females (Gilchrist, forthcoming), occurrences of postconception control (eviction, abortion, and infanticide) are rare, suggesting a similarly egalitarian distribution of postparturition reproductive success. Nonetheless, aspects of the occurrence of eviction, abortion, and infanticide have implications for social control of reproduction.

Reproductive competition between females may be an important factor driving eviction events: all female evictions occurred during estrus and gestation in groups with the largest number of reproductive females, all females that were evicted were of reproductive status, and all females that aborted were

allowed reentry to the group. The aggression and stress endured by evictees is likely to have been responsible for inducing abortion in those females that aborted while being evicted from their group (as in *Papio cynocephalus*, Wasser and Barash 1983). The higher incidence of abortion in young females is probably due to their vulnerability to stress (Gilchrist et al. 2004).

In the absence of an ability to suppress reproduction in rival breeders, eviction may be the only mode of limiting reproductive competition within the group. Johnstone and Cant (1999b) provide a model for control of reproduction by eviction, and this may be applicable to the banded mongoose, where eviction events have been recorded in the largest groups and appear to be associated with sexual competition rather than competition for food per se (Cant et al. 2001; Gilchrist 2001). However, the rarity of eviction and its restriction to the largest groups suggest that reproductive competition may be of negligible importance except at unusually high group sizes, for example, where a group has access to supplemental food. All evictions and the majority of abortions occurred in 2 groups (1b and 2) of the 3 with access to anthropogenic food sources (Gilchrist and Otafi 2002; Otafi and Gilchrist 2004).

Alternatively, the costs of eviction to the evictors may be so high as to make reproductive costs tolerable except at the largest group sizes. The costs to the evictors of evicting young reproductive individuals (that may be more prone to eviction due to their inexperience, smaller physical size, and probable subordinate status) could be in terms of direct fitness, through lost foraging time, risk of injury (both evictors and evictees were sometimes visibly wounded), and loss of reproductive fitness (during eviction events, 3 of 4 litters with pups less than 30 days old failed). Eviction of group members is also likely to be costly to an evictor's indirect fitness because evictees are usually relatives whose survival or future reproductive success is reduced by eviction (JS Gilchrist, unpublished data).

Few species show the high degree of within-group synchronization of parturition exhibited by banded mongooses: giving birth on the same day or week (Emlen and Demong 1975; Ims 1990; Clarke et al. 1992; Thompson 1995; but see Boinski 1987). This synchronization is especially interesting because younger females usually mate later than older females and would therefore be expected to give birth later (Cant 2000). The proximate cues triggering synchronization in banded mongoose appear to be strong, because females occasionally aborted some or all fetuses from a litter, apparently in an effort to synchronize parturition. In addition to the cases described in Results, on another occasion, on the date that a group gave birth, 2 miscarried fetuses were found near the den alongside a live neonate (this event was excluded from analyses of abortion because the mother's identity was unknown). Although the mechanisms that initiate labor in mammals are poorly understood (Lyle 1996), olfactory or pheromonal cues are thought to play a role in within-group synchronization (Boinski 1987; Thompson 1995).

There is additionally the possibility that a female does not necessarily give birth to her entire litter in a single parturition event but can give birth to her litter over different dates. To my knowledge, this is the first evidence for such behavior in a mammal. Three cases are described in Results. However, the strongest evidence that a female can give birth to a single litter over different dates is that one female was found to be gestating 2 of 5 fetuses (counted at palpation) after having apparently given birth (her abdomen changed from heavily swollen to flaccid overnight) in synchrony with other females. In this case, the communal litter was asynchronous (with approximately 3 days between the first and final female giving birth), and the female had apparently given birth with the first fe-

males (this event was not classified as an abortion because the female gave birth within the normal gestation period). These examples, highlighting premature parturition and parturition over different dates, suggest that there is strong selective pressure for synchrony of parturition or that premature parturition is a maladaptive response to a trigger from other females.

There are numerous potential selective pressures for synchronization of parturition (see aforementioned references and Rutberg 1987). However, in the banded mongoose and other cooperative breeders, economy and coordination of cooperative care for young in the communal litter (e.g., babysitting and provisioning; Cant 2003; Gilchrist 2004) or postparturition social control of reproductive success (e.g., infanticide) could be important factors.

For a female that is unable to control the fecundity of other females by suppressing conception or inducing abortion, there remains the possibility of postparturition control by infanticide. Infanticide of the offspring of other breeders has been recorded among a wide array of taxa, including many cooperative breeders (Hrdy 1979; Pusey and Packer 1987; Creel et al. 1997; Clutton-Brock et al. 1998; Ebensperger 1998). In meerkats and dwarf mongooses, subordinate litters are often killed by the dominant female, and the success of subordinate litters is affected by the timing of parturition, with a pregnant dominant female meerkat more likely to kill subordinate pups than a dominant female that has given birth (Rasa 1994; Creel and Waser 1997; Clutton-Brock et al. 1998, 2001). Similarly, egg tossing has been observed in communal laying bird species, in which the last female to start laying usually tosses the eggs already laid from the nest (Mumme et al. 1983; Vehrencamp et al. 1988; Koenig et al. 1995; Macedo and Bianchi 1997; Macedo et al. 2001).

If temporal cues are similarly important to infanticide in the banded mongoose, asynchronous litters should have a lower per capita success, and the last females to give birth should produce more emergent pups than those that give birth earlier. Litters where females give birth asynchronously are more likely to fail than when all females gave birth on the same day (Gilchrist, forthcoming), and a higher proportion of pups survive from birth to independence in synchronous than asynchronous litters (JS Gilchrist, unpublished data). Synchronizing parturition may obscure the cues used by a parent to differentiate between her own and others' offspring and may be especially advantageous to "subordinate" females in minimizing the risk of their pups being killed. For example, communal nesting female house mice, *Mus musculus domesticus*, differentiate between their own and other pups based on age differences but cannot differentiate when pups are matched for age (Manning et al. 1995).

Although infanticide represents a plausible ultimate cause for synchronized parturition, in banded mongooses, it is a rare occurrence. In 5 years of intensive observation of habituated groups, only 2 possible male intragroup infanticides have been observed (Cant 2000), and pup remains have been found in fecal samples from only 4 individuals across 2 communal litters. An alternative possible selective pressure for synchronization of parturition is that the offspring of females that give birth later are at a competitive disadvantage relative to early born pups. Mennella et al. (1990) showed that survival of younger litters of communal nursing Norway rats, *Rattus norvegicus*, was lower due to a competitive disadvantage in competition for milk. Similarly, numerous studies of birds show that in asynchronously hatching broods, late-hatched chicks are smaller and more likely to die (Amundsen and Stokland 1988; Pijanowski 1992). There may therefore be a trade-off, with early born pups (if they survive) having a competitive advantage over later born pups in access to nursing mothers' milk.

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