Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal

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Reproductive events in animal societies often show a high degree of temporal clustering, but the evolutionary causes of this synchronisation are poorly understood. Here, we suggest that selection to avoid the negative effects of competition with other females has given rise to a remarkable degree of birth synchrony in the communal-breeding banded mongoose (Mungos mungo). Within banded mongoose groups, births are highly synchronous, with 64 per cent of females giving birth on exactly the same night. Our results indicate that this extreme synchrony arises because offspring suffer an increased risk of infanticide if their mother gives birth before other females, but suffer in competition with older littermates if their mother gives birth after them. These findings highlight the important influence that reproductive competition can have for the evolution of reproductive synchrony.

Keywords: synchrony; infanticide; communal breeding; reproductive skew; offspring competition

1. INTRODUCTION

When females breed in groups, reproductive events such as oestrus, births or egg-laying are often more clustered temporally than can be explained by climatic seasonality alone [1]. Considerable research effort has focused on understanding the evolutionary causes of this synchronisation, with early hypotheses focusing on ways in which synchrony could improve offspring survival; for example, by reducing predation through a dilution or prey swamping effect, allowing more efficient communal care of young, or more efficient foraging by offspring (for a review, see [1]).

It has also been suggested that reproductive synchrony could minimize the negative effects of conflict with other breeding females. When females breed in groups, their offspring commonly compete for limited resources [2]. Synchronizing reproduction could maximize offspring survival in the face of this competition in two ways. First, by giving birth in synchrony, females may limit the ability of cobreeders to commit infanticide, since infanticidal females risk killing their own young [3,4]. Evidence in support of this hypothesis comes from observations that females are less likely to commit infanticide after they have given birth themselves [5,6]. Second, females can minimize the negative effects of competition with cobreeders by ensuring their own offspring will not be outcompeted for resources [2]. Females should therefore be under selection to give birth, before, or at the same time, as other females, to minimize the likelihood that their offspring will be smaller than their littermates.

Here, we investigate the influence of reproductive conflict on birth synchrony in the banded mongoose, a small (less than 2 kg) diurnal African carnivore that lives in stable multi-sex groups of 8–40 individuals. Banded mongooses provide an ideal opportunity to investigate the evolution of birth synchrony, as in each breeding attempt up to 10 females (mean = 3.75) become pregnant, and in 64 per cent of breeding attempts give birth on exactly the same night (figure 1). While females in other mammals often give birth within weeks [7], days [3] or even hours of each other [5] there are few other mammals where large numbers of females routinely give birth in such complete synchrony. This synchrony is even more remarkable in banded mongooses because females mate on different days, so the gestation period of females within the same breeding attempt can differ by up to one week [8]. Such extreme birth synchrony cannot be attributed to extrinsic environmental cues [9], and is unlikely to arise solely through predator avoidance, or a need to provide efficient care to young (although both factors are likely to be important in banded mongooses); since these advantages would also accrue when offspring are born within several days of each other. This raises the possibility that competition with other females and/or their offspring could help to explain the high degree of birth synchrony observed in banded mongoose societies.

Here, we investigate the influence of reproductive competition on birth synchrony in the banded mongoose. Previous work on this species has shown that litter survival is higher in synchronous litters (where all females give birth on the same day) than asynchronous litters (where females give birth over several days [10]). We extend this work, and investigate the causes of these benefits to offspring survival. We investigate the influence of synchrony on (i) offspring survival pre-emergence from the natal den, as this is when within-group infanticide occurs [8] and (ii) offspring survival when pups forage with the group (approx. 4–12 weeks post-birth), as this is when pup competition has a large influence on offspring survival [2]. If infanticide plays a role in the evolution of birth synchrony, we predict that offspring loss pre-emergence will be higher in asynchronous litters (owing to the loss of the offspring of early-birthing females), as females who have not yet given birth will be able to kill the offspring of other females without risking killing their own young. If minimizing offspring competition helps explain birth synchrony, we predict that offspring mortality post-emergence will be higher in synchronous litters (owing to the poor survival of the offspring of later-birthing females) as younger, smaller pups are likely to be outcompeted by older littermates.
sula, QENP, Uganda (0 12' S, 27 54' E) between November 1995 and
April 2008. Habitat and climate are described elsewhere [8].
All animals were marked individually and most groups were habitu-
tated to observation from less than 5 m. Pregnancy can be identified
at around 40 days by swelling of the abdomen [8] and birth dates can
be accurately determined by a sudden change in the female’s body
shape. We defned ‘any group’ as any group of births within 30 days in the same group, as pups born within this period
would be reared together in a communal litter [10]. If all pregnant
females gave birth on the same date, the breeding attempt was classi-
fi ed as ‘synchronous’, and if one or more females gave birth a day or
more apart, the breeding attempt was classifi ed as ‘asynchronous’.
Breeding attempts in which only one female gave birth within 30
days were excluded from analyses. Statistical analyses were per-
formed in GENSTAT 11.1 (VSN International Ltd, Hemel
Hempstead, UK). Details of all analyses are provided in tables of
the electronic supplementary material. Unless otherwise stated,
means are given ± 1 s.e.

2. MATERIAL AND METHODS

(a) Data collection

We studied 13 groups of banded mongooses living on Mweya Penin-
sula, QENP, Uganda (0 12’ S, 27 54’ E) between November 1995
and April 2008. Habitat and climate are described elsewhere [8].

Infanticide typically occurs in the den, so is rarely observed in our
population. Infanticide was observed on 24 occasions, in all cases
within one week of birth. To investigate the inluence of infanticide
on pre-emergence survival, we therefore looked at the survival of
individual litters in asynchronous breeding attempts during the first
week after birth. Litter survival could be monitored daily during
this period by recording whether or not the group left babysitters.

Pre-emergence offspring survival

Pups fi rst emerge from the den at 21 ± 6 days of age (mean ± s.d.;
n = 111 litters). To investigate whether birth synchrony infl uenced
the proportion of the communal litter lost pre-emergence, we ftted
the number of pups that emerged as the binomial response in a
GLMM with the total number of pups gestated by all pregnant
females as the binomial denominator. The number of pups gestated
was assessed by capturing females during pregnancy and estimating
the number of foetuses each carried by palpation (following Cant
[8]). Only communal litters where all pregnant females were cap-
tured were used, so our sample size for this analysis was restricted
to 12 synchronous and 11 asynchronous litters in eight groups.

Post-emergence offspring survival

Foraging pups compete aggressively with their littermates for adult
helpers (known as ‘escorts’), who provision and protect them [11].
Larger pups have a competitive advantage [2], which is likely to
decrease the survival of younger pups in asynchronous litters. We
compared the weight of pups that emerged frst in asynchronous lit-
ters (and were therefore assumed born frst) with those emerging
second, to demonstrate that at a given point in time, younger pups
were lighter than older pups. To investigate whether birth synchrony
influenced the proportion of emergent pups that survived to inde-
dependence (three months), we ftted the number of pups alive at
independence to a GLMM, with the number of emergent pups as
the binomial denominator. Whether the litter was synchronous
(n = 99) or asynchronous (n = 43) was ftted as the main term of
interest (n = 142 communal litters in 13 groups). We also compared
the proportion of frst-emerging pups that survived to independence
per litter with that of those emerging second.

3. RESULTS

(a) Birth synchrony and offspring survival pre-emergence

The proportion of pups lost between birth and emergence was signifi cantly lower in synchronous litters

Figure 1. Days asynchronous (days between frst and last
birth per litter) in 294 litters in which more than one
female bred.

Figure 2. The infl uence of (a) birth synchrony on the per cent
of pups lost before emergence; (b) reproductive timing on the
probability that pups survived the fi rst week; (c) birth synchrony
on the per cent of emergent pups that died before 3 months.

(i) Pre-emergence offspring survival

The proportion of pups lost before emergence (% )

(ii) Post-emergence offspring survival

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helpers (known as ‘escorts’), who provision and protect them [11].
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Birth synchrony and offspring survival

(b) Birth synchrony and post-emergence offspring survival

In asynchronous litters, younger pups were significantly lighter than their older littermates when weighed on the same day (paired t-test: emerged first = 238.6 ± 28.0 g, emerged second = 162.4 ± 20.5 g; t = 2.74, n = 7 communal litters, p = 0.034). Overall, a significantly smaller proportion of pups survived between emergence and independence in asynchronous litters than in synchronous litters (χ² = 10.82, p < 0.001; figure 2c). This appears to be due to the poor survival of later-born pups, as there was a strong trend for a smaller proportion of second-emerging pups to survive to independence (paired t-test: emerged first = 0.55 ± 0.11, emerged second = 0.30 ± 0.13; t = 2.17, n = 7 communal litters, p = 0.065).

4. DISCUSSION

Our results suggest that birth synchrony in banded mongooses arises because offspring are at an increased risk of infanticide if their mother gives birth before other females, and show poorer survival post-emergence if their mother gives birth after. Females are therefore likely to maximize offspring survival in the face of this competition by giving birth on the same night. Although few social vertebrates synchronize parturition to this extent, there is evidence that both the threat of infanticide and the need to minimize competition with other female’s young influence birth timing in other species. In some joint-nesting birds, for example, females toss eggs laid before their own from the nest [12] and many social mammals kill offspring born before their own, but allow offspring born after to survive [5,6]. In lions (Panthera leo) and Norway rats (Rattus norwegicus), offspring also show lower survival when reared with older offspring [7,13]. While we do not suggest that factors such as predator avoidance and efficient communal care are unimportant in banded mongooses, we believe that reproductive competition is the most likely explanation for the extreme birth synchrony observed in this species.

Selection for reproductive synchrony may be particularly strong in banded mongooses because pups must compete for access to adult escorts who provision and protect them. Small pups fare poorly in contests over escorts [2], generating strong selection for mothers to give birth as soon as other females produce surviving young. As mammalian young often grow faster post-parturition than in the latter stages of gestation [14], giving birth as soon as other females produce young may be the best way of minimizing offspring size differentials. Our findings highlight the important influence that reproductive competition can have for the evolution of reproductive synchrony, and demonstrate that extreme acts of coordination may result from selection to maximize individual fitness.

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