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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 synchronization 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 synchronization, 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 asynchronous 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.

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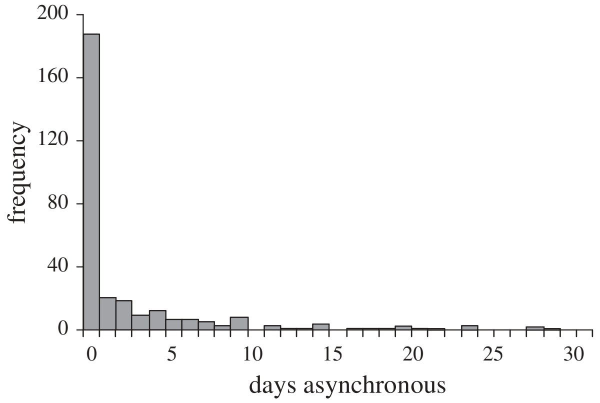

Figure 1. Days asynchronous (days between first and last birth per litter) in 294 litters in which more than one female bred.

2. MATERIAL AND METHODS

(a) *Data collection*

We studied 13 groups of banded mongooses living on Mweya Peninsula, 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 habituated 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 define a 'breeding attempt' 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 day, the breeding attempt was classified as 'synchronous', and if one or more females gave birth a day or more apart, the breeding attempt was classified as 'asynchronous'. Breeding attempts in which only one female gave birth within 30 days were excluded from analyses. Statistical analyses were performed 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.

(i) *Pre-emergence offspring survival*

Pups first emerge from the den at 21 ± 6 days of age (mean $\pm$ s.d.; $n = 111$ litters). To investigate whether birth synchrony influenced the proportion of the communal litter lost pre-emergence, we fitted 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 captured were used, so our sample size for this analysis was restricted to 12 synchronous and 11 asynchronous litters in eight groups.

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 influence 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. While other sources of mortality (e.g. starvation, predation) could also influence litter survival during this period, only mortality owing to infanticide is likely to vary consistently with reproductive timing. Additional variables likely to influence other mortality sources (e.g. group size and rainfall) were also controlled in our analyses (following Young & Clutton-Brock [6]). Whether each female's litter survived the first week after birth (1 = some pups survived, 0 = all died) was fitted as the binomial response in a GLMM. The timing of reproduction relative to other females in the group (first, middle and last) was fitted as the main term of interest ($n = 135$ birth events, 69 first, 18 middle, 48 last, by 79 females in 36 litters in 10 groups). Cases where females gave birth when another litter was already being babysat were excluded, as in these cases it was not possible to determine whether the second litter survived ($n = 42$).

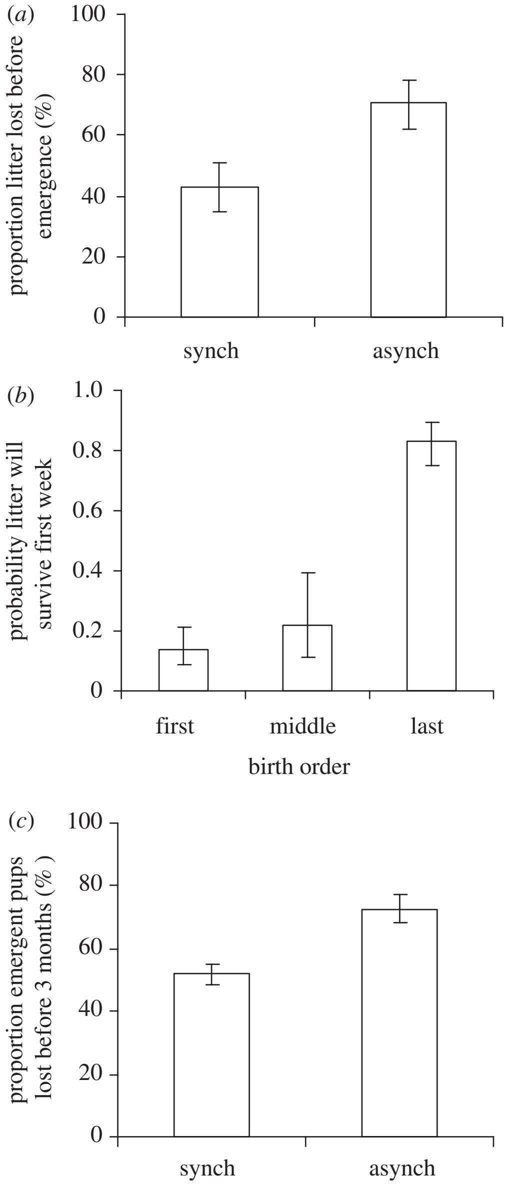

Figure 2. The influence of (*a*) birth synchrony on the per cent of pups lost before emergence; (*b*) reproductive timing on the probability that pups survived the first week; (*c*) birth synchrony on the per cent of emergent pups that died before 3 months.

(ii) *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 first in asynchronous litters (and were therefore assumed born first) 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 independence (three months), we fitted 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 fitted as the main term of interest ($n = 142$ communal litters in 13 groups). We also compared the proportion of first-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 significantly lower in synchronous litters

($\chi^2_1 = 5.1$, $p = 0.035$; figure 2*a*), although even in synchronous litters pup mortality was high (40%). The order of birth in asynchronous litters had a strong influence on survival, with litters born before other females having a significantly lower probability of survival than those born later ($\chi^2_2 = 33.11$, $p < 0.001$; figure 2*b*).

(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 ($\chi^2_1 = 10.82$, $p < 0.001$; figure 2*c*). 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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