



Original Article

# Reproductive conflict resolution in cooperative breeders

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Female infanticide is common in animal societies where groups comprise multiple co-breeding females. To reduce the risk that their offspring are killed, mothers can synchronize breeding and pool offspring, making it hard for females to avoid killing their own young. However, female reproductive conflict does not invariably result in reproductive synchrony, and we lack a general hypothesis explaining the variation in conflict resolution strategies seen across species. Here, we investigate the fitness consequences of birth timing relative to other females and the prevalence of birth synchrony in cooperatively breeding Kalahari meerkats (*Suricata suricatta*). We show that, although there would be substantial benefits to females in synchronizing births and reducing their risk of infanticide, birth synchrony is rare. Since precise breeding synchrony has evolved in a related species with similar infanticidal female reproductive conflict, its absence in meerkats requires an evolutionary explanation. We therefore explore the costs and benefits of synchronizing breeding in two theoretical models, each of which contrasts synchrony with an alternative reproductive strategy: (i) breeding opportunistically and accepting fitness losses to infanticide or (ii) suppressing the reproduction of others to prevent infanticide. Our models show that the costs of synchrony constrain its development if subordinates breed infrequently, and that selection instead favors the suppression of subordinate reproduction by the dominant and opportunistic reproduction by subordinates. Together, our results suggest that the resolution of reproductive conflict in animal societies is shaped by differential breeding propensities among female group members, leading to divergent conflict resolution strategies even in closely related species.

**Key words:** birth synchrony, cooperative breeding, infanticide, meerkat, reproductive conflict, reproductive synchrony.

## INTRODUCTION

Intense reproductive conflict among females is commonplace where multiple co-breeding females live in stable groups (Clutton-Brock 2009; Clutton-Brock and Huchard 2013; Stockley and Campbell 2013), and in its most extreme form, this reproductive conflict results in mothers killing young that would reduce resource availability for their offspring (Blumstein 2000; Digby and Saltzman 2009; Lukas and Huchard 2019). Such female infanticide is taxonomically widespread, and reproductively active females are far more likely perpetrators (Hoogland 1985; Hansson et al. 1997; Rödel et al. 2008; Digby and Saltzman 2009; Nelson-Flower et al. 2013; Schmidt et al. 2015; Riehl 2016), generating intense

reproductive conflict among co-breeding females in a social group (Lukas and Huchard 2019). Though the resolution of reproductive conflict among infanticidal females clearly has fitness consequences for group members, we lack an understanding of the factors that determine how this is achieved.

Infanticidal reproductive conflict among breeding females can be resolved by at least three strategies. First, individuals may simply accept the risk of suffering fitness losses to infanticide and breed opportunistically (Hager and Johnstone 2004). Second, one or more individuals may suppress the reproduction of others to limit their propensity of becoming infanticidal (Digby and Saltzman 2009; Young 2009). Non-breeding females typically do not commit infanticide, and reproductive suppression therefore allows the dominant female(s) to reproduce with minimal risk of their offspring being killed or outcompeted. Where suppression is realized, within-group aggressive interactions are occasionally observed (but not always, Cant et al. 2014). The third strategy for resolving infanticidal conflict is synchronous breeding (Poikonen et al. 2008; Hodge et al. 2011; Riehl 2016). Synchronized parturition or egg-laying and the

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resulting pooled offspring reduce the incentives to commit infanticide by confusing offspring identity such that mothers risk killing their own young (Riehl 2016). In both mammals and birds, infanticide by females is rare when females synchronize reproduction (Cant et al. 2014; Riehl 2016; Lukas and Huchard 2019). However, females breeding too early (both naturally and experimentally induced) suffer high rates of infanticide (Cant et al. 2014; Riehl 2016), while females that breed too late risk their young being outcompeted by older, larger rivals (Hodge et al. 2011). Breeding synchrony effectively avoids these tandem forms of reproductive conflict.

While empirical observations indicate a strong evolutionary link between reproductive conflict among co-breeding females, infanticide, and breeding synchrony (Poikonen et al. 2008; Schmaltz et al. 2008; Hodge et al. 2011; Schmidt et al. 2015; Riehl 2016), theoretical work has typically treated each of these in isolation. First, most theory relating to female reproductive conflict focuses on the sharing of reproduction within groups (i.e., reproductive skew, Johnstone 2000; Nonacs and Hager 2011) without addressing infanticide risk or breeding synchrony. Second, explicit models of infanticide investigate the conditions under which committing infanticide confers benefits (Johnstone and Cant 1999; Hager and Johnstone 2004), but assume that the underlying conflict resolution strategy is one of suppression (with varying effectiveness), neglecting potential conflict mitigation by other strategies. Finally, arguments for the adaptiveness of breeding synchrony under the threat of infanticide are largely based on verbal models and implicitly assume limited control of subordinate reproduction by dominants (Riehl 2016; but see Schmidt et al. 2015 for a notable exception). Thus, there currently exists no direct contrast between fundamentally different reproductive strategies to resolve within-group conflict in the same theoretical framework, and we consequently lack hypotheses for which factors favor one strategy over others.

Here, we use a long-term study of wild Kalahari meerkats (*Suricata suricatta*), to investigate the costs and benefits of birth synchrony for subordinate females with respect to infanticide risk. We then examine the extent to which parturitions are synchronized. Meerkats live in obligately cooperatively breeding groups of up to 50 individuals (median = 16; Kutsukake and Clutton-Brock 2010), and are an ideal study species to address the resolution of female reproductive conflict in animal societies. While subordinates breed at lower frequency than the single dominant female, any mature subordinate is a potential reproductive competitor, and this conflict can result in both costly pup competition and infanticide (Clutton-Brock et al. 1998; Russell et al. 2002; Cram et al. 2017). Our preliminary analysis showed that breeding synchrony is rare in meerkats, despite intense reproductive conflict among females (Clutton-Brock et al. 2006) and the repeated evolution of reproductive synchrony in other cooperative breeders, including close relatives of the meerkat (Hodge et al. 2011; Riehl 2016). To account for our empirical findings, we build two simple theoretical models to evaluate how ecological and social conditions affect the fitness benefits of birth synchrony compared to two alternative reproductive strategies: suppression of subordinate reproduction by dominants and opportunistic breeding by subordinates. We discuss how these factors may generate the diversity of reproductive conflict resolution strategies exhibited in group-living vertebrates.

## MATERIALS AND METHODS

### Field system

Data collection was conducted in the context of a long-term study monitoring a naturally regulated population of wild meerkats at the

Kuruman River Reserve, South Africa (26°58'S, 21°49'E), between 1994 and 2015. A single dominant male and female monopolize reproduction in each group (producing 86% and 93% of all pups, respectively; Griffin et al. 2003; Spong et al. 2008), but subordinates of both sexes also attempt to breed (Young et al. 2007; Bell et al. 2014). Both dominant and subordinate females can perpetrate infanticide and have their litters killed in this species (Young and Clutton-Brock 2006). All study individuals were individually tagged (Five Star ID, Johannesburg, South Africa), habituated to close observation (<1 m), and visually recognizable using small dye marks (Clutton-Brock and Manser 2016). Groups were visited two to three times per week for 4–8 h, to collect behavioral, life-history, body weight, and group composition data. Observations of pregnancy, birth, infanticide, dominance, and group size were made using protocols detailed elsewhere (Griffin et al. 2003; Young and Clutton-Brock 2006; Hodge et al. 2008). Briefly, pregnancy could be confirmed following a swelling of the abdomen and nipples and concomitant weight gain, parturition was identified by sudden weight loss and change in body shape, and infanticide was defined as the loss of an entire litter in the birth burrow during the 4 days following birth.

### Ethical note

The data in this study are from behavioral observations of habituated wild meerkat groups, where disturbance caused by our presence is likely to be minimal. We closely monitored meerkat welfare while collecting body weights data, applying non-toxic hair dye marks, and capturing individuals for transponder chip fitting. All protocols were designed to minimize impacts on the study animals, and have been approved by the Animal Ethics Committee of the University of Pretoria.

### Statistical analysis

Statistical analyses were carried out in R v. 3.2.3, using a full model approach (R Development Core Team 2013). The significance of terms was tested using maximum log-likelihood estimation following removal of the term from the full model. Data are available from Dryad (Cram et al. 2019).

### *How does parturition timing, relative to other female group-mates, affect subordinate litter survival?*

To test whether timing of parturition, relative to the pregnancy status of other females in the group, affected infanticide risk for subordinate litters, we ran a generalized linear mixed-effects model (GLMM) with a binomial distribution, using the package “lme4” (Bates et al. 2015). The response was a binary term stating whether a subordinate litter was killed in the 4 days following birth or not. The two predictors of interest were the pregnancy status of the dominant female (binary: pregnant or not), and the number of other subordinates pregnant (continuous covariate) at the time the focal subordinate gave birth. We also tested for other factors which could determine the probability of a subordinate’s litter surviving: the age of the subordinate, the age of the dominant female, and the number of adults in the group (hereafter “group size”). These covariates were recorded at subordinate conception. We did not include the weights of the mother or dominant female, or ecological parameters (e.g., temperature, rainfall, season) as previous work has shown these do not influence infanticide risk in this species (Young and Clutton-Brock 2006). All predictors were standardized so that the resulting coefficients are directly comparable following Gelman (2008). The random terms were subordinate female ID (to control

for females who gave birth multiple times in our dataset: 273 pregnancies from 192 subordinate females) and group ID (to control for multiple subordinates giving birth in the 22 social groups).

### *Do subordinate females synchronize parturition with the dominant female?*

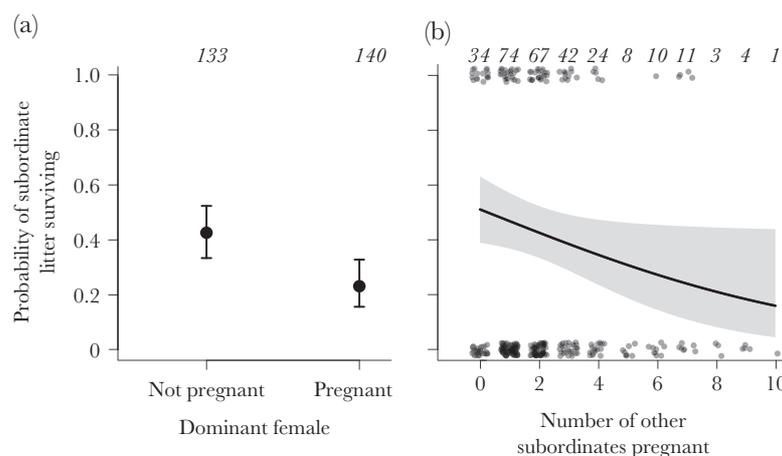
To investigate whether subordinate females synchronize parturition with the dominant female, we extracted a dataset of subordinate parturitions that occurred within 30 days before or after a dominant female parturition (before or after,  $n = 260$  births from 201 subordinate females). We chose 30 days either side of the dominant's parturition as this 61-day period provides a wide enough observation period to estimate the distribution of subordinate parturitions, but prevents ambiguous results arising if a female gives birth twice within a single period (because meerkat gestations are typically 70 days and thus parturition cannot happen twice in a 61-day period; Sharp et al. 2013). We assigned each subordinate parturition a value according to how many days until or since the nearest dominant parturition (0 being perfect synchrony, 1 being subordinate parturition the day after the dominant etc.). We tested whether the number of subordinates giving birth in synchrony with their dominant female was greater than expected by chance alone, using one-tailed two-proportion  $Z$ -tests. If the 260 subordinate births in our dataset were uniformly distributed across the 61-day observation period for each pregnancy (30 days either side of the dominant and perfect synchrony), we would expect approximately four subordinates to give birth on any given day. We first compared the observed number of subordinates giving birth on the same day as their dominant female with this null value. We then repeated this analysis to test for evidence that subordinates were unsuccessfully attempting to synchronize with the dominant, and were giving birth close to the dominant but not in perfect synchrony. We compared the observed number of females giving birth within 1 or 2 days either side of their dominant's birth with the expected number for a random 3- or 5-day period, respectively. We also tested whether subordinates were more likely than chance to give birth in the 2 days after, or 2 days before, the dominant's parturition. Finally, if subordinate births are clustered loosely in time around dominant

births (indicating approximate or unsuccessful birth synchrony), we would expect the distribution of absolute days between subordinate and dominant births to be skewed towards zero rather than uniform. We used a Kolmogorov–Smirnov test whether the distribution deviated from uniformity, with the package “uniftest” (Melnik and Pusev 2015).

### Theoretical models

We model an individual's life time reproductive success ( $W$ ; i.e., the total number of surviving offspring) as a function of a maximum number of offspring an individual can produce ( $\varphi$ ). For subordinates this number is scaled according to their propensity to breed ( $\beta$ ), that is, their ability to acquire matings and subsequently produce offspring. Breeding propensity thus encapsulates both subordinate quality and access to mates relative to the dominant. We define offspring as having survived if they avoid infanticide, which typically takes place in the days immediately following birth or egg-laying (Young and Clutton-Brock 2006; Riehl 2016). Infanticide is perpetrated by co-breeding females ( $\varepsilon$ : number of potentially co-breeding females): a mother's offspring will fall victim to infanticide if other pregnant females are present (see Figure 1). Below, we contrast alternative breeding strategies that individuals can adopt under the threat of infanticide, and how the number of co-breeding females in a group and their propensity to breed influences which of these strategies is favored.

Our models are built with a number of underlying, general assumptions that help keep them simple: first, we focus on the effects of infanticide on reproductive success, assuming that all other factors that will influence reproduction affect all individuals equally. As such,  $\varphi$  implicitly incorporates any effect that could reasonably be argued to impact reproductive success, for example, environmental conditions or species-specific fecundity. Second, we assume that any reproductive benefits accrued in larger groups with more breeding females (e.g., from improved foraging or reduced predation) are the same under any reproductive strategy. We hence do not include any term describing the relationship between  $\varphi$  and  $\varepsilon$  other than those that model the risk of infanticide. Third, we interpret  $\beta$  as an abstract, relative



**Figure 1**

(a) The probability a subordinate female's litter will survive its first few days is substantially decreased if it is born before the dominant female has given birth. Model predictions and 95% confidence intervals, with number of other subordinates pregnant held at the median (two females). (b) Similarly, the probability a subordinate female's litter will survive is substantially decreased if the litter is born while more subordinates are pregnant when she gives birth. Model predictions and 95% confidence intervals, with the dominant female not pregnant at the time of subordinate parturition. Points show raw data, jittered and translucent for clarity, and italicised numbers denote litter sample sizes.

measure of subordinate quality, and the resulting probability that reproductive conflict occurs among group members: higher values of  $\beta$  increase subordinate breeding propensity (Equations 1–2) and consequently increase their likelihood of engaging in infanticide (Equation 1; Clutton-Brock et al. 2008), as well as increasing the costs of suppressing their reproduction (Equation 4; Bell et al. 2012, 2014). Conversely, higher values of  $\beta$  reduce the costs of synchrony (Equations 2 and 5). While the effects of variation in  $\beta$  accrue in different currencies (e.g., pups lost, energy spent on suppression, or number of foregone reproductive opportunities), we take the simplest approach to contrasting the impact of  $\beta$  on reproductive strategies by including it as a scaling factor in all our equations. Fourth,  $\beta$  also implicitly incorporates subordinates' ability to acquire matings: we define subordinate breeding propensity  $\beta$  as a composite measure of the likelihood of subordinate reproduction, influenced by their access to mates and their ability to expend time and energy reproducing. Fifth, we limit our calculation of reproductive success to offspring survival shortly after birth or egg-laying, once infanticide ceases to be a risk (e.g., Young and Clutton-Brock 2006; Rödel et al. 2008; Schmidt et al. 2015; Riehl 2016). We thus do not address how reproductive strategies may impact offspring survival on longer timescales.

#### Model 1: subordinates' reproductive strategies: opportunistic breeding versus birth synchrony

We compare two behavioral strategies for subordinates: subordinates either accept the loss of a certain proportion of their reproduction to infanticide by other breeding females in the group (opportunistic reproduction; Equation 1) or synchronize their own reproduction with that of all other group members (birth synchrony; Equation 2)—all other females are assumed to be breeding opportunistically and synchrony changes the focal individual's breeding attempts to those times when the breeding attempts of all other group members are aligned. Under opportunistic subordinate reproduction, a subordinate female's maximum reproductive output ( $\varphi * \beta$ ) is reduced by a factor proportional to the combined cost of suffering from infanticide by the dominant female ( $\kappa_{DF}$ ) or other breeding subordinates ( $\kappa_{SF}$ ; scaled by their number [ $\varepsilon - 2$ ] and propensity to breed [ $\beta$ ]). Note that we infer both values from our empirical data (Figure 1): dominant pregnancy halves subordinate reproductive success, each additional pregnant subordinate reduces it by about 5% (see Figure 3). Lifetime reproductive success of subordinates that breed opportunistically ( $W_{SF[\varnothing]}$ ) is then given as:

$$W_{SF[\varnothing]} = \varphi * \beta * (1 - \kappa_{DF}) * (1 - \kappa_{SF} * \beta)^{\varepsilon - 2} \quad (1)$$

Under birth synchrony, subordinates lower their reproduction by a factor that is proportional to the number and breeding propensity of other females in the group ( $\beta^{\varepsilon - 2}$ ; note that we assume dominant female breeding propensity to be 1. A subordinate synchronizing with a dominant thus incurs no lost opportunity cost). Life time reproductive success of subordinates that synchronize their reproduction with all other group members ( $W_{SF[s]}$ ) is then given as:

$$W_{SF[s]} = \varphi * \beta * (\beta^{\varepsilon - 2}) \quad (2)$$

Thus, the reproductive success differential between the two strategies available to subordinates is:

$$\Delta W_{SF} = W_{SF[\varnothing]} - W_{SF[s]} \quad (3)$$

Here, positive values (i.e.,  $W_{SF[\varnothing]} > W_{SF[s]}$ ) indicate that opportunistic reproduction is more beneficial, while negative values indicate benefits of birth synchrony (i.e.,  $W_{SF[\varnothing]} < W_{SF[s]}$ ). By calculating  $\Delta W_{SF}$  for different values of  $\varepsilon$  and  $\beta$ , we can identify how the number of co-breeding females and their propensity to breed determine which of the two strategies should be favored under different social conditions.

#### Model 2: dominants' reproductive strategies: suppression of subordinates versus birth synchrony

We assume that two reproductive strategies exist for dominant females: first, they can suppress the reproduction of other females. We assume that suppression is costly to dominants (see Figure 3; Bell et al. 2012, 2014), and that these costs increase with the number of subordinates in a group (Clutton-Brock et al. 2008). Thus, suppression is modeled to reduce maximum reproductive output ( $\varphi$ ) by a factor proportional to the relative breeding propensity of subordinates ( $\beta$ ) and their number in the group ( $\varepsilon - 1$ ). Lifetime reproductive success of dominants that suppress subordinates' reproduction ( $W_{DF[\rho]}$ ) is then given as,

$$W_{DF[\rho]} = \varphi * \left( \frac{1}{1 + \beta * (\varepsilon - 1)} \right) \quad (4)$$

Second, a dominant female can synchronize her own reproduction with other females, thus lowering her own frequency of breeding, but avoiding the risk of infanticide. Her lifetime reproductive success under synchrony ( $W_{DF[s]}$ ) is then given as:

$$W_{DF[s]} = \varphi * (\beta^{\varepsilon - 1}) \quad (5)$$

Again, we can calculate the reproductive success differential between the two strategies available to dominants ( $\Delta W_{DF}$ ) as:

$$\Delta W_{DF} = W_{DF[\rho]} - W_{DF[s]} \quad (6)$$

Here, positive values (i.e.,  $W_{DF[\rho]} > W_{DF[s]}$ ) indicate that suppression of subordinates is more beneficial, while negative values indicate benefits of birth synchrony (i.e.,  $W_{DF[\rho]} < W_{DF[s]}$ ).

## RESULTS

### How does parturition timing, relative to other female group-mates, affect subordinate litter survival?

The timing of a subordinate female's parturition relative to that of the dominant female significantly predicts the survival of the subordinate's litter (GLMM:  $\chi^2_1 = 9.95$ ,  $P = 0.002$ ,  $n = 273$  litters, Figure 1a). Litters born to subordinates while the dominant female is pregnant have a substantially higher probability of being killed before they emerge from the natal burrow, compared with those born after the dominant female has given birth (Figure 1a). Controlling for the significant effect of the dominant female's pregnancy status, the probability of a subordinate's litter surviving to emergence was also significantly predicted by the pregnancy status of other subordinate females (GLMM:  $\chi^2_1 = 4.54$ ,  $P = 0.03$ , Figure 1b). When more subordinate group-mates are pregnant at the time of a given subordinate's parturition, infanticide is more frequent and the probability of litter survival is decreased (Figure 1b). The effects of the pregnancy status of co-breeding group-mates (both dominant and subordinate) on a female's litter survival should lead to birth synchrony: mothers will be selected to delay parturition until other females in the group have given birth, and then

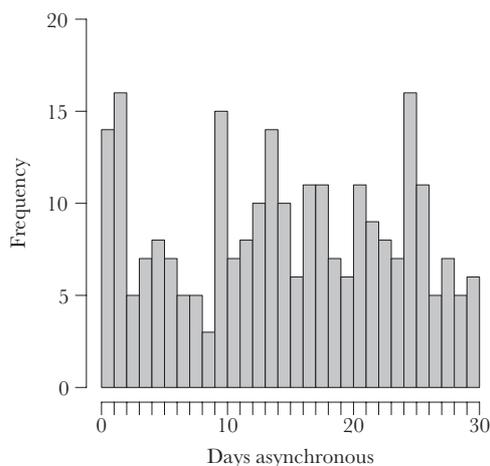
give birth immediately. A subordinate female's litter survival was not significantly predicted by her age at conception, the dominant female's age, or the group size (GLMM, all  $\chi^2_1 < 2.93$ ,  $P > 0.09$ , see [Supplementary Table S1](#)).

### Do subordinate females synchronize parturition with the dominant female?

Despite the apparent benefits of synchrony for litter survival, we found no evidence that subordinate females synchronize parturition with the group's dominant female or with each other ([Figure 2](#)). Subordinate females were no more likely than chance to give birth on the same day as their dominant female (one-tailed two-proportion  $\chi^2$ -test:  $\chi^2 = 0$ ,  $P = 0.5$ ), or in the 2 days before, or after, or within 1 or 2 days either side of the dominant's parturition (all  $\chi^2 < 1.39$ ,  $P > 0.12$ ). Overall, only 4% of subordinates that gave birth within 30 days of their dominant female were synchronized perfectly, compared to 65% in banded mongooses (*Mungos mungo*; [Hodge et al. 2011](#)). There was equally no evidence of a tendency towards approximate synchronicity, as the frequency distribution did not significantly differ from uniformity (Kolmogorov–Smirnov test for uniformity:  $D = 0.89$ ,  $P = 0.95$ , [Figure 2](#)).

### How do the number of co-breeding females, and their propensity to breed, determine the fitness consequences of birth synchrony compared to other reproductive strategies?

Analysis of our theoretical models shows that differences in breeding propensity among co-breeding females, represented in our models by  $\beta$ , strongly influence which reproductive strategy is favored ([Figure 3](#)): where subordinates breed infrequently (i.e., low values of  $\beta$ ), they almost always benefit from opportunistic reproduction, while dominant fitness is maximized by suppressing, rather than synchronizing with, their subordinates. Conversely, where differences in breeding propensity are less pronounced (i.e., high values of  $\beta$ ), both subordinates and dominants achieve higher reproductive success when synchronizing for most numbers of co-breeding females we consider here. The optimal behavioral reproductive strategies, that is, synchrony or opportunism/



**Figure 2**  
Frequency histogram of the absolute number of days between a subordinate female's parturition and the nearest parturition of the group's dominant female. See supplementary materials for a similar figure showing natural, rather than absolute, number of days between subordinate and dominant births.

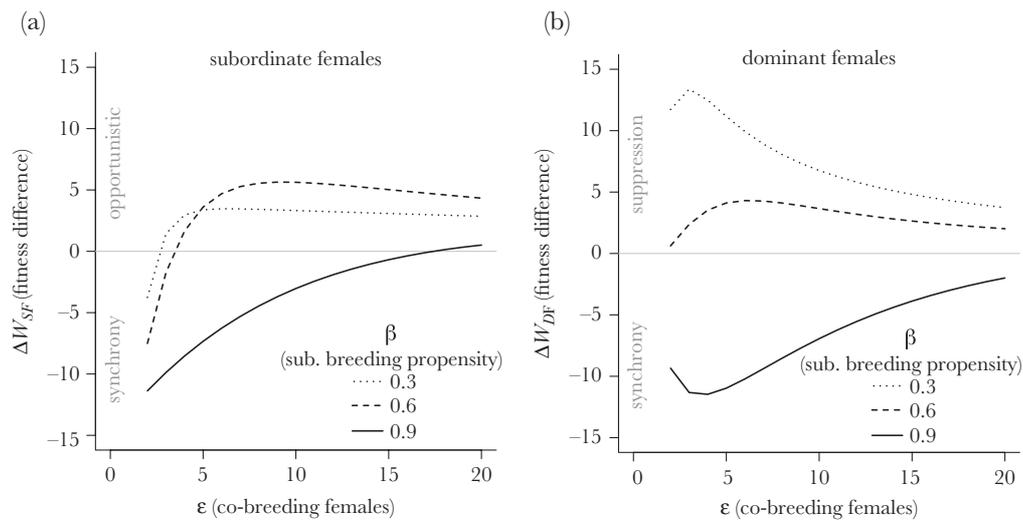
suppression, are thus typically aligned between subordinates and dominants for extreme values of  $\beta$  (solid vs. dotted lines in [Figure 3](#)). The number of potentially co-breeding females in a group ( $\epsilon$ ) also influences whether dominant and subordinate strategies are aligned or not, especially for intermediate values of  $\beta$  (dashed lines in [Figure 3](#)): for groups with only two co-breeding females ( $\epsilon = 2$ ), subordinates always prefer synchrony as it incurs no costs to them (see “Methods”), but dominants only do so for relatively high values of  $\beta$ . Conversely, synchrony stops being favored for subordinates for fewer co-breeding females than the respective switching point for dominants.

## DISCUSSION

Our empirical results reveal that birth synchrony is rare in meerkats, despite yielding clear fitness benefits for subordinates by improving litter survival. The infrequency of synchrony is especially surprising considering that a closely related species, the banded mongoose, exhibits extreme birth synchrony in most breeding episodes ([Hodge et al. 2011](#)). To explore possible explanations for why banded mongooses (as well as other social vertebrates, [Riehl 2016](#)) exhibit reproductive synchrony but meerkats do not, we analyzed simple theoretical models with respect to conditions that favor synchrony over alternative strategies (i.e., opportunistic reproduction by subordinates and/or suppression of subordinate reproduction by dominants). Our models reveal that breeding synchrony yields lower benefits where group members differ greatly in their breeding propensity, as the opportunity costs incurred by synchrony are elevated, and the costs of suppression or suffering from infanticide are relatively low. By contrast, increases in subordinate breeding frequency elevate the costs of suppression and risk of infanticide while reducing the opportunity costs of synchrony, leading to group-wide synchronization of reproduction. We discuss our empirical and theoretical results with respect to strategies for conflict resolution in animal societies, and the ecological and social factors that may have contributed to contrasting strategies adopted by meerkats and other social vertebrates.

In subordinate female meerkats, we found no evidence that births were synchronized with the dominant female. This lack of synchrony is surprising for three reasons. First, giving birth too late exacerbates pup competition (as offspring then compete with older pups), and previous work in meerkats has shown that nutritional competition among pups can lead to reduced growth rates and shortened telomeres, which can in turn affect survival and fitness later in life ([English et al. 2013](#); [Cram et al. 2017](#)). Second, giving birth too early leads to an elevated risk of infanticide, resulting in complete loss of the litter ([Figure 1](#)). As such, we would expect strong selection for birth synchrony. Finally, a close relative of the meerkat, the banded mongoose, shows extreme birth synchrony, whereby 65% of females typically give birth on the same day ([Hodge et al. 2011](#)). Given the clear benefits of birth synchrony in meerkats, and its evolution in a closely related social mongoose, why do not subordinate meerkats synchronize their births with those of other breeding females?

Using simple models, we explored how subordinate female breeding propensity affects the fitness consequences of different reproductive strategies under the threat of infanticide: for subordinates, we contrasted birth synchrony with opportunistic reproduction where females accept the loss of some litters to infanticidal group-mates. For dominants, we contrasted birth synchrony with costly suppression of subordinate reproduction. We find that synchrony is



**Figure 3**

Predictions of the theoretical models for which reproductive strategy should be favoured by subordinates (a; model 1) or dominants (b; model 2). Negative values of  $\Delta W$  (y-axis) in both plots indicate higher life time reproductive success for birth synchrony, positive values indicate either benefits of opportunistic reproduction for subordinates (a) or benefits of suppressing subordinate reproduction for dominants (b). Models were run for 2–20 potentially co-breeding females ( $\epsilon$ ; x-axis) and for three different values of subordinate breeding propensity ( $\beta$ ; dotted, dashed, and solid lines – see legends;  $\varphi$  set to 25;  $\kappa_{DF}$  set to 0.5 and  $\kappa_{SF}$  set to 0.05 – see Figure 1 and Methods: model 1).

favoured in both subordinates and dominants under some conditions and detrimental under others: in groups composed of females with similar breeding propensity (i.e., where subordinates are of high quality and readily have access to mates, indicated in our models by high values of  $\beta$ ), synchrony is often beneficial. Conversely, in groups with large differences in breeding propensity among females (low values of  $\beta$ ) subordinates should usually favor opportunism and dominants typically benefit from suppression. These differences in optimal reproductive conflict resolution strategy arise because increased subordinate breeding propensity reduces the costs of breeding synchrony, but increases the costs of suppression and infanticide.

Our models also suggest that the number of breeding females can exert an important influence on the fitness pay-offs of the contrasting conflict resolution strategies, especially for intermediate values of  $\beta$ . For dominants, the net benefits of synchrony reduce rapidly with increasing numbers of co-breeding females because the opportunity costs of delaying reproduction to synchronize with all of them are high. Conversely, the costs a dominant incurs from actively suppressing additional subordinate females increase comparably slowly, favoring suppression in large groups for most values of  $\beta$ . For subordinates, opportunism is favored over synchrony as the number of breeding females increases. Again, this arises from contrasts in how the costs of the different strategies change with the number of co-breeding females: the costs of synchrony are low in smaller groups but increase rapidly with additional co-breeding females, while the costs of opportunism rise more steadily (note that this finding holds for a wide range of values of  $\kappa_{DF}$  and  $\kappa_{SF}$ ). Our models therefore highlight that two factors, number of competitors and relative breeding propensity differences among them, are sufficient to favor either of the different reproductive strategies under the risk of infanticide.

Our findings will help direct future theoretical work aiming to clarify the evolution of contrasting strategies to resolve reproductive conflict among females. Specifically, we identify three limitations in our models, which could fruitfully be addressed in future work:

first, feedbacks between different strategies employed by group-mates may alter a strategy's costs and benefits. For example, if several females are already synchronized, the costs of synchronizing with them are reduced. Second, while infanticide risk is likely the primary selective pressure driving birth synchrony, offspring competition may also play a role (Hodge et al. 2011; Riehl 2016). Late-born offspring may face a reduced risk of infanticide, but are likely to compete with offspring older than themselves, which may hinder their development and reduce their fitness. Finally, other biological systems may require the addition of other variables not considered here, or adjustments to the functions describing the costs and benefits of divergent reproductive strategies.

Nevertheless, natural variation in conflict resolution strategies observed between species can be understood in the light of our theoretical models. Banded mongoose societies (in which females typically synchronize births) include relatively high numbers of females that breed frequently, while meerkat groups (in which such synchrony is rare) have fewer subordinate females with lower breeding propensities (Cant 2000; Kutsuk and Clutton-Brock 2008; Cant et al. 2016). These divergent group compositions, which we explicitly analyze in our model, likely arise due to key ecological differences between banded mongooses and meerkats: meerkats inhabit the arid Kalahari Desert, while banded mongooses live in more verdant grassland and forest, usually close to water (Cant et al. 2016; Clutton-Brock and Manser 2016). This contrast in ecological conditions has two consequences for subordinate reproduction. First, subordinate female meerkats are typically in poor physical condition and do not conceive as frequently as subordinate banded mongooses. Subordinate meerkats are further constrained because they rarely have access to within-group unrelated mates and avoid inbreeding (O'Riain et al. 2000), whereas banded mongooses inbreed frequently (Nichols et al. 2014). In combination, this probably favors opportunistic reproduction whenever a subordinate female is simultaneously in sufficiently good condition to conceive and has access to unrelated sperm. Second, the poor condition of subordinate meerkats likely makes them more amenable to aggressive

reproductive suppression by the dominant female. Together, subordinate meerkats' infrequent conceptions and limited ability to resist suppression likely result in reduced benefits of birth synchrony for the dominant female, and lower costs of suppression (although these costs are still detectable as reduced maternal and pup weight, Bell et al. 2014).

Similarly, among other cooperatively breeding vertebrates, species with distinct quality asymmetries among group members (resulting in pronounced dominance hierarchies) appear to favor active suppression, while those with more egalitarian societies synchronize reproduction. In pied babbblers (*Turdoides bicolor*), subordinates almost never reproduce in their natal group, partly due to a lack of unrelated partners and partly due to the frequent aggression they receive from dominants (Nelson-Flower et al. 2013). In contrast, aggression is rare in groups of anis (*Crotophaga major*), and multiple breeding females regularly produce mixed clutches (Schmaltz et al. 2008; Riehl 2016). It is notable, however, that infanticide is observed in both systems: in response to opportunistic reproduction by subordinate pied babbblers, and asynchronous egg-laying in anis (Schmaltz et al. 2008; Riehl 2016). Among cooperatively breeding callitrichid monkeys, infanticide risk is strongly influenced by birth timing, and relative breeding propensity of female group members appears to determine whether reproductive conflict is resolved by active suppression or largely synchronized reproduction (Digby and Saltzman 2009; Digby et al. 2010). In cooperatively breeding cichlid fishes, larger subordinate females are more fecund and better able to withstand aggression (Heg and Hamilton 2008; Dey et al. 2013), and consequently reproduce in parallel with dominants (Heg and Hamilton 2008). Smaller subordinates are instead reproductively suppressed by aggression and infanticide (in the form of egg eating; Heg and Hamilton 2008).

Both the empirical findings presented here and our theoretical models suggest the potential for an evolutionary feedback loop between within-group quality differences among competitors and the adoption of either synchrony or suppression/opportunism as a conflict resolution strategy: where subordinates are of poor quality, the dominant is likely to be selected to suppress them, further reducing their propensity to breed, and thus lowering the costs of suppression for the dominant even further. By contrast, where subordinates are in good condition, refraining from suppression and synchronizing reproduction is beneficial for dominants, which may further increase subordinates' propensity to reproduce, reducing the costs of synchrony for all group members. In this verbal evolutionary feedback model, reproductive skew is thus both cause and effect of quality differences and the entailing conflict resolution strategies within animal societies (Johnstone 2000).

In conclusion, our results suggest that co-breeding females can exert a strong negative effect on the reproductive success of their rivals, even in groups of closely related females. Infanticide of rival litters is perhaps the most extreme manifestation of female reproductive conflict, and the probability of a female's offspring being killed is largely determined by the timing of her parturition relative to those of other breeding females. Conflict between potentially infanticidal females can be resolved either through reproductive suppression of subordinate females by one or more dominant females combined with opportunistic reproduction by subordinates, or by birth synchrony among all females. Our theoretical models suggest that group traits likely play a key role in determining how reproductive conflict is resolved in animal societies, with the outcome largely determined by subordinates' breeding propensity.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Cram et al. (2019).

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