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## RESEARCH ARTICLE

# Pregnancy reduces concurrent pup care behaviour in meerkats, generating differences between dominant and subordinate females

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## Abstract

1. In some mammals, and particularly in cooperative breeding ones, successive bouts of reproduction can overlap so that a female is often pregnant while still nurturing dependent young from her previous litter. Such an overlap requires females to divide their energetic budget between two reproductive activities, and pregnancy costs would consequently be expected to reduce investment in concurrent offspring care. However, explicit evidence for such reductions is scarce, and the potential effects they may have on work division in cooperative breeders have not been explored.
2. Using 25 years of data on reproduction and cooperative behaviour in wild Kalahari meerkats, supplemented with field experiments, we investigated whether pregnancy reduces contributions to cooperative pup care behaviours, including babysitting, provisioning and raised guarding. We also explored whether pregnancy, which is more frequent in dominants than subordinates, could account for the reduced contributions of dominants to the cooperative pup care behaviours.
3. We found that pregnancy, particularly at late stages of gestation, reduces contributions to cooperative pup care; that these reductions are eliminated when the food available to pregnant females is experimentally supplemented; and that pregnancy effects accounted for differences between dominants and subordinates in two of the three cooperative behaviours examined (pup provisioning and raised guarding but not babysitting).
4. By linking pregnancy costs with reductions in concurrent pup care, our findings illuminate a trade-off between investment in successive, overlapping bouts of reproduction. They also suggest that some of the differences in cooperative behaviour between dominant and subordinate females in cooperative breeding mammals can be a direct consequence of differences in their breeding frequency.

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## 1 | INTRODUCTION

In many mammal species, including cooperative breeding ones, there can be an overlap between consecutive bouts of reproduction such that females are often pregnant while still nurturing their previous offspring (rodents: Carrillo-Martinez et al., 2011; Dewsbury, 1990; Gilbert, 1984; McKenna et al., 2021; bats: Happold & Happold, 1990; Lucan et al., 2014, tenrecs: Stephenson & Racey, 1993; horses: Bartosova et al., 2011, peccaries: Mayor et al., 2006, pinnipeds: Trillmich & Wolf, 2008; dolphins: West et al., 2007; giraffes: Deacon et al., 2015, rhesus macaques: Lee et al., 2019; cooperative breeders: Clutton-Brock & Manser, 2016; Roellig et al., 2011; Tardif et al., 2003). Since animals typically have limited resources for reproduction, life history theory predicts that there is likely to be a trade-off between investing in current versus future reproduction (Stearns, 1992). When consecutive reproduction bouts overlap, this trade-off accentuates as the energetic budget needs to be divided concurrently between care for young and pregnancy costs, predicting a reduction in investment in both; that is, pregnancy would be expected to reduce investment in concurrent care for young and vice versa. Correspondingly, short interbirth intervals were found to decrease survival of both preceding and succeeding offspring in rhesus macaque *Macaca mulatta* (Lee et al., 2019), and lactating mothers in several species shorten their lactating period if they are pregnant in parallel (Duncan et al., 1984; Gomendio, 1991; Green et al., 1993). Nevertheless, while current versus future reproductive trade-offs have been widely demonstrated by showing that high investment in a reproductive bout reduces investment in the following nonoverlapping one (Fisher & Blomberg, 2011; Hanssen et al., 2005; Lee et al., 2019; Nilsson & Svensson, 1996; Rivalan et al., 2005), the effects of pregnancy on concurrently nurturing previously born young were studied only scarcely (DelBarco-Trillo & Ferkin, 2006; Gomendio, 1991; Green et al., 1993; Naguib et al., 2010), and, as yet, their potential effect on the division of work in cooperative breeding mammals has not been explored.

In cooperative breeders, the task of rearing young is shared among multiple individuals, lightening the rearing effort of parents and allowing the breeding female to reduce her investment in offspring care (e.g. Clutton-Brock et al., 2004; Hatchwell, 1999; Heinsohn, 2004; Houston & Davies, 1985; Koenig & Dickinson, 2016). Correspondingly, interbirth intervals of breeding females in cooperative breeding species are significantly shorter than in noncooperative breeders (Lukas & Clutton-Brock, 2012). Reductions in offspring care while pregnant could facilitate shorter interbirth intervals, yet this has not been tested in cooperative breeders.

In several singular cooperative breeding mammals, like meerkats and social mole-rats, where a single dominant female per group virtually monopolize reproduction and subordinates rarely breed, dominant females commonly contribute less to cooperative behaviours than subordinates (Clutton-Brock et al., 2004; Houslay et al., 2020; Lacey & Sherman, 1991). Although workload differences of this kind are sometimes interpreted as an incipient form of caste differentiation (Alexander et al., 1991; Jarvis & Bennett, 1993; Scantlebury

et al., 2006; but see Zöttl et al., 2016), as found in eusocial insects (Wilson & Holldobler, 2005), an alternative possibility is that these differences are a direct consequence of differences in breeding frequency between dominant and subordinate females and their associated energetic costs.

In this paper, we investigate the effects of pregnancy on cooperative pup care in Kalahari meerkats. We use 25-year data collected on meerkat pregnancy status and cooperative behaviour (Huchard et al., 2016), as well as field experiments involving the manipulation of pregnancy status (by contraceptive injections; Bell et al., 2014) and food availability during pregnancy (by food supplementation; Dubuc et al., 2017). Our research aims to determine whether pregnancy costs reduce contributions to cooperative pup care behaviours (provisioning, babysitting and guarding), whether this accounts for the lower contributions of dominant females which are pregnant more frequently than subordinate females (Clutton-Brock et al., 1998, 2004; Huchard et al., 2016), and whether pregnancy shorten the mother's lactating period.

Meerkats live in groups of  $13 \pm 6.3$  individuals (mean  $\pm$  SD in our study population) with a single dominant pair that monopolize reproduction and produce over 80% of the surviving young born in the group (Huchard et al., 2016; Spong et al., 2008). The dominant female monopolizes reproduction through aggressive interactions towards subordinate females and infanticide of their offspring (Clutton-Brock et al., 2001; Young et al., 2006), yet subordinates also get pregnant occasionally (Young et al., 2006). All group members contribute to the cooperative pup care activities including babysitting, pup provisioning and raised guarding (see Section 2). Lactation is sometimes shared between the mother and allolactating females but they contribute less than mothers (MacLeod et al., 2015), and pups start eating also solid food at age of ~4 weeks (Clutton-Brock & Manser, 2016) and wean completely at age of ~7.5 weeks. Since pregnancy lasts around 70 days (Doolan & Macdonald, 1997), conception usually occurs a few days after giving birth, and pups do not reach nutritional independence until the age of ~90 days (Huchard et al., 2016), it is common for dominant females to be at advanced stages of pregnancy when their previous litters are still nutritionally dependent. As in many other mammals, fetuses grow very little during the first half of gestation period in meerkats, and growth increases rapidly during the second half of gestation, reaching its maximum shortly before birth (Sharp et al., 2013). As a result, pregnancy costs would be expected to have little effect on cooperative behaviour during the first half of the gestation period but to have increasing impact during the second half of the gestation period.

Using long-term records of the life histories of 631 individuals from 40 groups monitored by the Kalahari meerkat project (Huchard et al., 2016), we investigated whether the contributions of dominants and subordinates to different forms of cooperative pup care (pup feeding, babysitting and raised guarding) differed between non-pregnant, early pregnant (first half of pregnancy) and late-pregnant (second half) females. We hypothesized that the energetic costs of gestation would reduce contributions to cooperative pup care by females, especially in the later stages of gestation, when energetic

requirements are higher (Sharp et al., 2013), and would shorten the lactating period. We also explored the (known) differences in cooperative contributions between dominants and subordinates with and without accounting for pregnancy status to deduce whether pregnancy status may account for these differences. Finally, two previous experiments conducted in the same study population allowed us to explore the consequences of manipulating pregnancy costs for cooperative behaviour. In the first, subordinate females were temporarily prevented from becoming pregnant using contraceptive injections (Bell et al., 2014), allowing us to test if they contributed more to pup care than control females (treated with saline injections) that became pregnant. In the second experiment, dominant females were experimentally provided with supplemental food during late pregnancy (Dubuc et al., 2017), allowing us to compare their pup care behaviour to control (unfed) females and assess whether food constraints were responsible for the effects of pregnancy on contributions to pup care.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The data analysed here were collected from a meerkat population at the Kuruman River Reserve, South Africa, between 1995 and 2019 as part of the long-term Kalahari meerkat research (Huchard et al., 2016). Animals in the study population are tagged with transponder chips and are individually recognizable by small dye marks on their fur. They are habituated to close observation and the majority (>95%) are trained to get onto an electronic weighing balance. Meerkat groups are visited and observed three to five times a week throughout the year, for 3 h in the morning from the time the group leave the burrow and for an hour prior to the group returning to the burrow in the evening (Duncan et al., 2019). During group visits, behavioural data on cooperative behaviours are recorded ad lib (details below), and animals are weighted (at dawn; after 3 h of foraging; and at dusk). All study procedures were approved by the Animal Ethics Committee of the University of Pretoria, South Africa (no. EC010-13) and by the Northern Cape Department of Environment and Nature Conservation, South Africa (FAUNA 1020/2016).

### 2.2 | Life history data

Detailed records are kept on the individuals' life histories including their birth dates ( $\pm 1$ –2 days), group membership, pregnancies, lactation and dominance status (Duncan et al., 2018; Huchard et al., 2016). Pregnancies, which lasts for 70 days (Doolan & Macdonald, 1997), were detected  $36 \pm 10$  days before birth (mean  $\pm$  SD) from abdominal swelling and associated weight gain (Clutton-Brock et al., 2010; Sharp et al., 2013). Birth was identified by sudden change in body shape, dramatic weight loss (of 20% of the mother's weight prior to parturition, Sharp et al., 2013) and the onset of babysitting and

lactation behaviours (Dubuc et al., 2017; Hodge et al., 2008; Sharp et al., 2013). As behavioural signs of oestrus were rarely observed (Dubuc et al., 2017; Sharp et al., 2013), conception date was retrospectively estimated by backdating 70 days from birth (as in: Bell et al., 2014; Hodge et al., 2008; Sharp et al., 2013). Pregnancies were presumed to end in abortions when terminated prematurely without babysitting and lactation signs to indicate pup presence. In such cases (27%), conception date was estimated by backdating 35 days from pregnancy detection date. Lactation was clearly identified from obvious presence of damp, sandy, suckle mark rings around the nipples of lactating females (MacLeod et al., 2015). The dominant female is identified from frequency and direction of aggressive and submissive interactions within the group (see details in: Bell et al., 2014; Duncan et al., 2018) as well as from relative frequency of anal marking, which is substantially higher in dominants than subordinates (Thavarajah et al., 2014).

### 2.3 | Cooperative behaviour

Using ad lib observations, we examined individual contributions to three cooperative activities: (1) babysitting, where during the first 3–4 weeks of the life of litters at least one adult stays with the pups at the birth burrow throughout the day while the rest of the group forage. During this period groups were visited once or twice a day (morning and afternoon) and babysitting group members were recorded; (2) pup provisioning, occurring when pups join the group foraging forays but are not yet nutritionally independent. Pup provisioning data were restricted to the main provisioning period, which is the first 45 days after the pups first joined the group's foraging; and (3) guarding or 'sentinel duty' events, where an individual provides sustained vigilance for potential dangers from a raised position while the group members are foraging. Guarding data were also restricted to the pup provisioning period to concentrate on the cooperative pup-defence motive of guarding (Santema & Clutton-Brock, 2013) over the selfish ones (see Clutton-Brock et al., 1999).

In addition to ad lib observations, focal observations were collected throughout the long-term study, in which a focal animal was followed for 20 or 30 min and all its behaviours were recorded (see details in: Bell et al., 2014; Santema & Clutton-Brock, 2013). Using 2196 focal observations conducted on 41 dominant females during 205 pup provisioning periods, we extracted the proportion of prey items they donated to pups from total items they have obtained (generosity) to examine whether it was affected by pregnancy.

### 2.4 | Experiment 1: Subordinate contraception experiment

In July 2009–July 2011, a contraception experiment was held in our study population, in which subordinate females were injected with the contraceptive hormone Depo-Provera (medroxyprogesterone acetate) to prevent conception (Bell et al., 2014). In

six experimental groups, all subordinates above 180 days were treated with contraceptive injections every 3 months ( $n=35$ ; see details in Bell et al., 2014), and in six control groups, all subordinates were injected with an equivalent volume of saline solution ( $n=38$ ). In year 2, the same protocol was repeated, switching treated and control groups (Bell et al., 2014). Here, we used the data from this experiment to compare the pup care behaviour of females that were experimentally prevented from becoming pregnant ( $n=54$ ) contrasted with that of control females that were: not pregnant, early pregnant or late pregnant ( $n=50, 20, 16$ , respectively, Table S9).

## 2.5 | Experiment 2: Experimental feeding of pregnant dominants

In August–November 2011 and August–November 2012, 10 dominant pregnant females were experimentally fed during their second half of their pregnancy with one hen's egg a day (Dubuc et al., 2017). The controls in this experiment were all other successful pregnancies by dominants that ended in these periods, as well as pregnancies by females used in the experiment that ended in August–November the year before or after the year when they were experimentally fed (see Dubuc et al., 2017, for full description of this experiment). Here, we used this experiment to investigate differences in provisioning and guarding behaviours between fed, late-pregnant dominants ( $n=6$ ) and unfed control dominants that were either not pregnant or in the early or late stages of pregnancy ( $n=9, 10, 7$ , respectively, Table S10). The number of fed pregnant females that we analysed is lower than the number that were fed in the experiment (6 vs. 10 respectively) because our examination was restricted to periods when dependent pups were present. Additionally, contributions to babysitting could not be examined due to insufficient sample sizes ( $n=3$  for fed late-pregnant females).

## 2.6 | Data analysis

Pup provision events and guarding events per individual per ad lib observation session were based only on observation sessions longer than 30 min. They included 50,501 observations of pup feeding from 631 individuals during 522 breeding sessions. To analyse babysitting contributions, a binary variable indicating if the individual was babysitting (yes/no) was extracted from observation sessions during babysitting periods.

We used GLMMs to test pregnancy status (not pregnant, early pregnant and late pregnant) effects and their interaction with dominance status on individual contributions per observation session to the three cooperative activities (provisioning, guarding and babysitting). We additionally controlled for the following variables: (1) age (months); (2) group size—the number of individuals over 6-month age in the group; (3) pup number; (4) pups age (days); (5) rainfall—accumulated rainfall in the preceding 3 months (details in: Rotics &

Clutton-Brock, 2021); (6) lactation status (yes/no); and (7) observation session time (am/pm). The maximal models also included: (a) quadratic terms for all continuous predictors, as their effects are often nonlinear (Clutton-Brock et al., 2004; Duncan et al., 2019); (b) an interaction of each predictor with dominance status to allow different parametrization for dominants and subordinates as they greatly differ in age, frequency of being pregnant and social behaviour (Clutton-Brock et al., 2004; Huchard et al., 2016); and (c) random factors for individual ID and litter ID. The random factor 'litter ID' is a unique identifier per reproduction session and this allows the model to also account for the variation due to other random factors such as group ID and year. The maximal models were then reduced to best fit models using stepwise selection based on the Akaike information criteria (AIC).

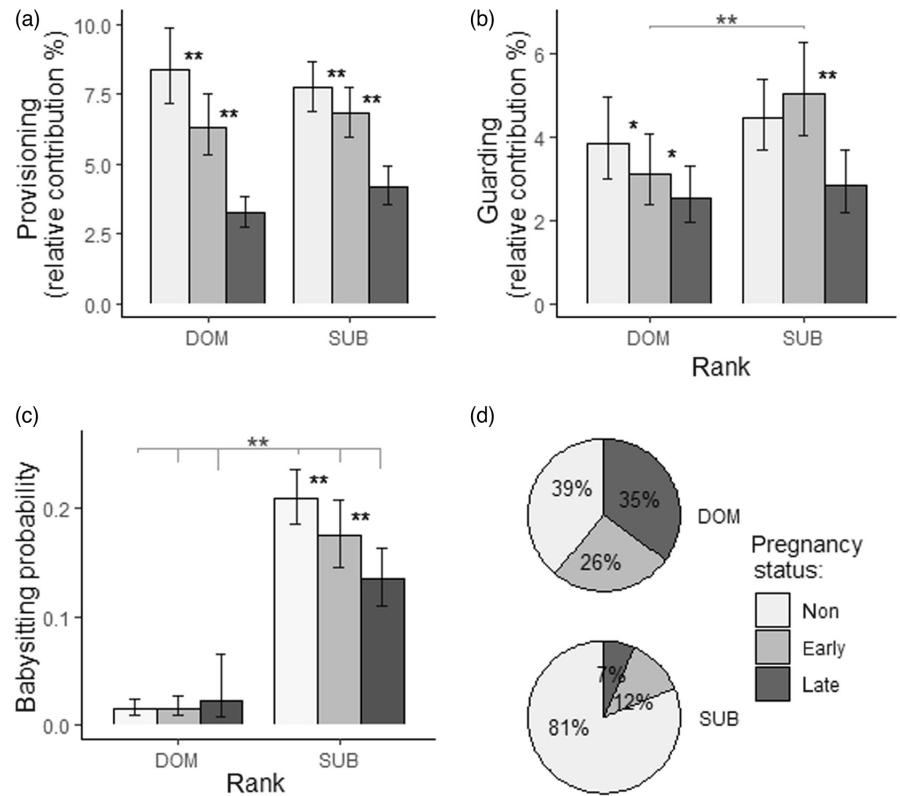
Relative individual contributions to pup provisioning and guarding per session were examined (separately) using GLMMs with negative binomial error distribution and zero inflation factor (applied across all observations,  $z_i = -1$ ), where the log total group provisioning or guarding, respectively, was included as an offset in the model. Including the group totals as an offset means that the relative individual contribution from the group contribution is examined. We additionally examined the absolute contributions—results did not change qualitatively and are provided in the Supporting Information (SI Text, Table S11, Figure S1 and S2). Pregnancy effects on individual babysitting probabilities per session were examined using GLMM with a binomial error distribution. Proportion of food items that dominant females donated to pups from the items they have found (based on the focal observations data) were examined using a GLMM with negative binomial error distribution and zero inflation factor, and the log total food items found were included as an offset in the model.

To model continuous changes throughout pregnancy (day 1–70) in pup provisioning and in pregnant female weight, we used GAMMs with binomial error distribution and with Gaussian error distribution respectively.

We also tested for a trade-off between pregnancy and lactation by examining whether dominant females that became pregnant when lactating terminated their lactation period earlier; we used an LMM model with lactation duration as a response variable, the predictors: pregnancy (yes/no), litter size, group size, age, rainfall and ID as random factor.

To explore whether the (known) differences in cooperative contributions between dominants and subordinates (Clutton-Brock et al., 2004) could be explained by pregnancy effect (which is more frequent in dominants; Young et al., 2006), we model each cooperative behaviour without accounting for pregnancy status (reported in Figure S3) and with accounting for pregnancy status, (as described above, reported in Figure 1) and checked whether accounting for pregnancy eliminates the differences between them. We further reported the differences in pregnancy probability (yes/no) during the pup provisioning period between dominants and subordinates, which was modelled using a similar GLMM model structure as reported above with a binomial error distribution.

**FIGURE 1** Effects of pregnancy on cooperative behaviours. Estimated marginal means  $\pm$  CI<sub>95</sub> are presented for (a) relative provisioning, (b) relative guarding and (c) babysitting probability of dominants of average age (4.7 years) and subordinates of average age (1.8 years) based on GLMMs detailed in [Tables S1–S3](#). For provisioning and guarding, relative contributions out of the total group execution of the behaviour are displayed (analyses of absolute contributions show similar results and are provided in [Figure S1, Table S11](#)). Plot (d) shows the distribution of pregnancy statuses in dominant and in subordinate females (age > 1 year) during the pup provisioning period. \*, \*\* mark significant differences ( $p < 0.05$ ,  $< 0.001$  respectively) between pregnancy statuses within dominance rank, and between dominance ranks of the same pregnancy status (see [Tables S1–S3](#), for full statistical details).



The effects of the two experimental manipulations on cooperative behaviours were tested using same models specified above for relative provisioning, relative guarding and babysitting probability. The experimental treatment and the pregnancy status were combined to one factor of four levels: treated group, which is contraceptive subordinates in *experiment 1* or fed pregnant dominants in *experiment 2*, and three control groups of: non-, early- and late-pregnant control females. The treated group was set as the reference level in the models and its contrasts with the three control groups were tested (see Section 3).

All continuous predictors in the analyses were scaled. Residuals' fit to the expected distribution and the absence of heteroscedasticity were verified using the DHARMA package (Hartig, 2019). We verified no multicollinearity by testing that variance inflation factors (VIFs) were less than 3 (Zuur et al., 2009). Even though in all our models  $VIF < 3$ , it is important to note that some models ([Tables S1–S3](#)) included the predictors 'dominance status' and 'age' that were correlated ( $r = 0.75$ ). Based on Morrissey and Ruxton (2018), there is no statistical fault in correlated predictors, but cautious is needed when interpreting their results—see in [Supporting Information Text](#) more explanations on how this was addressed and why we choose to include these correlated predictors. Data were processed in Matlab (The MathWorks Inc., version: 9.0.0.341360 [2016]) and statistically analysed in R3.6 using glmmTMB (Magnusson et al., 2017) and GAM (Wood, 2011).

### 3 | RESULTS

The contributions of females to most forms of cooperative pup care decreased when they were pregnant. Late-pregnant females

contributed less to pup provisioning, guarding and babysitting than nonpregnant and early pregnant females, within both dominants and subordinates ([Figure 1a–c, Table S1–S3](#)), with the exception of dominant contributions to babysitting, which were very low irrespective of pregnancy status. We also found reduced contributions in early pregnant females versus nonpregnant ones in provisioning (both in dominants and subordinates), in guarding (only in dominants) and in babysitting (only in subordinates), though these were smaller than differences between late-pregnant and nonpregnant females ([Figure 1a–c](#)). The proportion of food items that dominant females gave to pups from the ones they found (their 'generosity') was also lower in late-pregnant than early pregnant and nonpregnant females ([Figure 2, Table S4](#)). Throughout the first half of gestation, female contributions to pup feeding decreased slowly and then decreased rapidly, coinciding with the patterns of body weight gain during gestation ([Figure 3, Tables S5 and S6](#)).

Pregnancy also affected lactation period duration, which is on average  $52.4 \pm 8.4$  days, and dominant females that became pregnant while lactating terminated their lactation period 2.6 days earlier ( $\beta = -2.62 \pm 0.76$ ,  $p < 0.001$ , [Table S7](#)).

Pregnancy probability was much lower in subordinates than in dominants ( $\beta = -3.02 \pm 0.24$ ,  $p < 0.001$ ; [Figure 1d, Table S8](#)). Without accounting for pregnancy status, dominants contributed less than subordinates to all cooperative behaviours ([Figure S3, Clutton-Brock et al., 2004](#)), but when pregnancy status was accounted for, this largely eliminated the differences between dominants and subordinates in provisioning and guarding, though not in babysitting ([Figure 1](#)).

The results of two field experiments provided support for the findings of pregnancy effects on pup care. In the first, subordinate females that were prevented from becoming pregnant by contraceptive injections contributed more to provisioning and to guarding than control (saline jab) late-pregnant females (provisioning: Figure 4, Table S9; guarding:  $\beta = -0.57 \pm 0.26$ ,  $p = 0.03$ , Table S9), and did not differ from control nonpregnant and early pregnant females ( $p \geq 0.23$ , Figure 4, Table S9). The contributions of contraceptive-treated females to babysitting differed only from early pregnant controls ( $\beta = -0.39 \pm 0.19$ ,  $p = 0.04$ ) and not from late ones ( $\beta = -0.04 \pm 0.17$ ,  $p = 0.82$ ; Table S9), possibly because low sample size (both in terms of

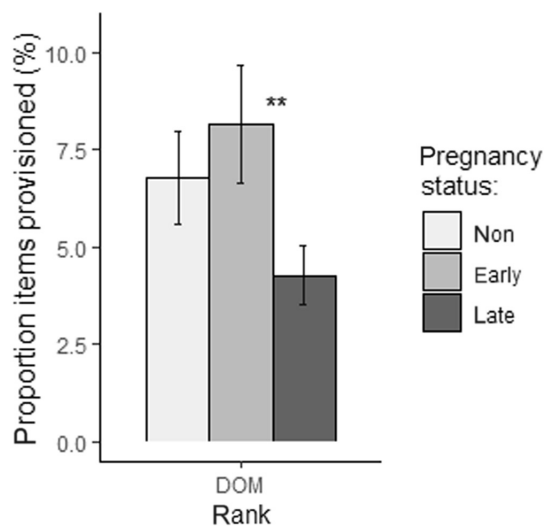


FIGURE 2 The proportion of food items that dominant females provisioned to pups from the ones they found (generosity), calculated from focal observations of dominant females during different stages of pregnancy. Estimated marginal means  $\pm$  SE are presented based on the GLMM detailed in Table S4; \*\* marks significance of  $p < 0.001$  between a bar and all bars to its left.

number of pregnant females:  $n = 17$  for both early- and late-pregnant females [Table S9] and number of events per individual:  $5.6 \pm 5.5$  per breeding bout; mean  $\pm$  SD) might have made identification of statistically significant differences rather stochastic.

In the second experiment, late-pregnant dominants that were experimentally provided with supplemental food contributed more to provisioning than control (unfed) late-pregnant dominants, and no differently from control nonpregnant and control early pregnant dominants (Figure 4, Table S10). Additionally, experimentally fed late-pregnant dominants contributed to guarding more than control late- and early pregnant dominants (late:  $\beta = -1.75 \pm 0.48$ ,  $p < 0.001$ ; early:  $\beta = -1.51 \pm 0.47$ ,  $p = 0.001$ ), and no differently from control nonpregnant dominants ( $p = 0.09$ , Table S10).

## 4 | DISCUSSION

Both our correlative and experimental results show that during the second half of pregnancy female meerkats reduce their contributions to cooperative pup care behaviours including provisioning, raised guarding and in subordinate females, also babysitting (dominant females hardly contribute to babysitting whether or not they are pregnant). Experimentally supplementing food to pregnant females eliminated these reductions, indicating that the association between pregnancy and reductions in pup care has a causal basis.

As far as we know, there are only a few records of pregnancy effects on maternal care in the wild. In feral horses and bison, pregnancy was found to reduce maternal care in the form of reduced lactating and earlier weaning of offspring (Cameron et al., 2000; Duncan et al., 1984; Green et al., 1993), which is corresponding to our finding that female meerkats terminate their lactating period earlier when pregnant (2.6 days earlier when the average is

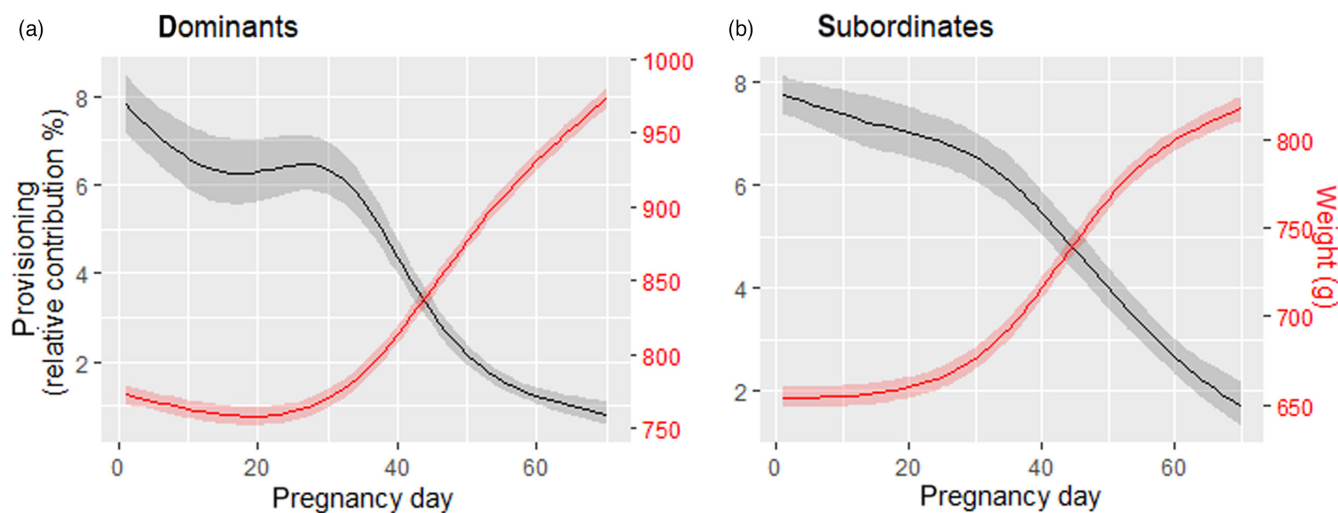
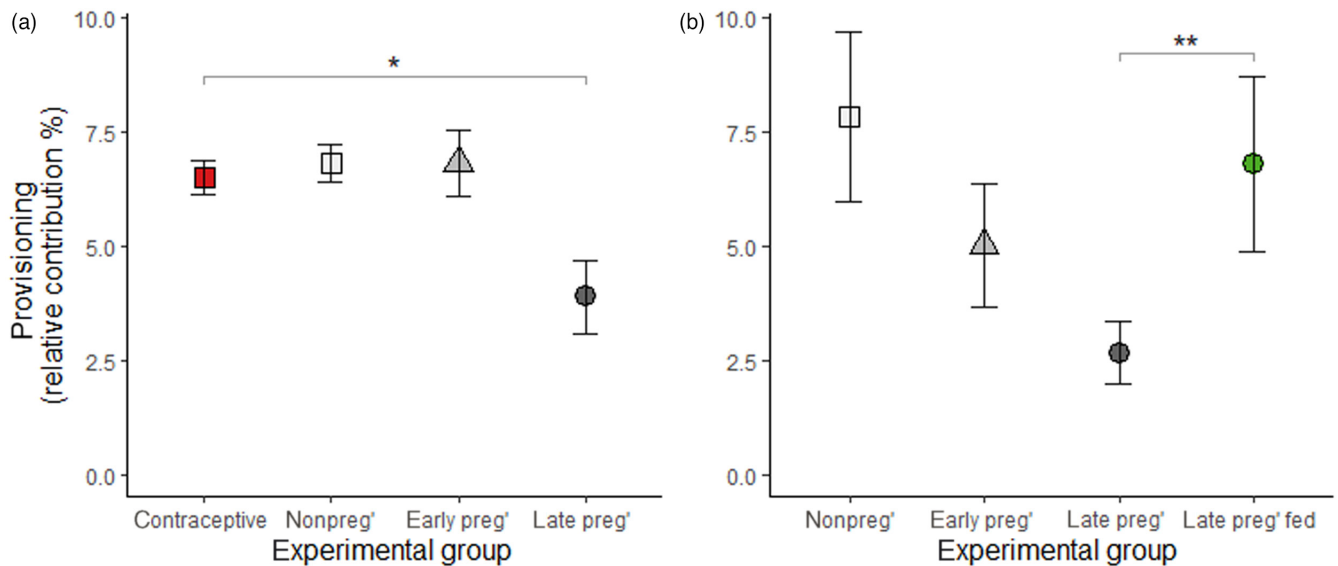


FIGURE 3 Changes throughout gestation in pregnant female rates of pup feeding (calculated as the proportion of pup feeding by the pregnant female from total pup feeding; black) and in pregnant females body weight (red) in: (a) dominants ( $n = 95$ ) and (b) subordinates ( $n = 610$ ). Lines and shaded areas mark predicted means and 95% CI based on the GAMs detailed in Tables S5 and S6.



**FIGURE 4** Effects of two pregnancy-related, experimental manipulations on relative contributions to provisioning (relative contribution from total group provisioning). (a) Subordinate females treated with contraceptive injection to prevent pregnancy ( $n=54$ ) versus control (saline jab) subordinate females which were: non, early and late pregnant ( $n=50, 20, 16$  respectively); (b) dominant females that were experimentally fed during late pregnancy ( $n=6$ ) versus control unfed dominant females that were: non, early and late pregnant ( $n=7, 10, 9$  respectively). Estimated marginal means  $\pm$  SE are presented based on the GLMMs detailed in [Tables S7 and S8](#). Statistical significance is marked only for differences between treated and control groups with \*, \*\* for  $p < 0.05$ ,  $p < 0.01$  respectively. Analysing the absolute contributions to provisioning gave equivalent results that are provided in the appendix ([Figure S2, Table S11](#)).

52 days). Related findings in primates show that the return of post-partum oestrus increases the mother rejection behaviour towards its infants (Berman et al., 1993; Collinge, 1987; Zhao et al., 2008). The relationships between pregnancy and maternal care have also been investigated in captive populations, though here results are inconsistent, showing negative effects of pregnancy on lactating in rhesus macaques (Gomendio, 1991) and on responsiveness to pup calls in guinea pigs (Naguib et al., 2010) but no negative effects of pregnancy on lactating frequency in domestic horses (Bartosova et al., 2011) and on litter growth rate in meadow voles (DelBarco-Trillo & Ferkin, 2006); it is possible that access to plentiful food in captivity mitigates the energetic costs of pregnancy. Thus, our study provides one of the clearest evidences that pregnancy reduces concurrent care for young.

Reductions in the contributions of pregnant meerkats to pup rearing could be seen as a particular case of the classic trade-off between investment in current versus future reproduction (Stearns, 1992). When time gaps between successive, nonoverlapping, reproduction bouts are long, studies typically find that high investment in first reproductive bout reduces investment in the following one (e.g. Fisher & Blomberg, 2011; Hamel et al., 2011; Hanssen et al., 2005; Nilsson & Svensson, 1996; Persson, 2005; Siefferman & Hill, 2005). However, when time gaps between successive reproduction bouts are short it appears that investment in both bouts decreases leading to reductions in survival of offspring from both preceding and succeeding bouts (Lee et al., 2019). The pregnancy effects in meerkats supplement that when the two bouts overlap, investment in subsequent litter (i.e. gestation) can reduce investment in the current one.

There are several benefits to breeding females from cooperative breeding lifestyle and reducing pup care while pregnant might be an additional one. One of the straightforward benefits to parents in cooperative breeders is lightening the offspring rearing effort via help from multiple group members (e.g. Clutton-Brock et al., 2004; Hatchwell, 1999; Heinsohn, 2004; Houston & Davies, 1985; Koenig & Dickinson, 2016). Recently it was shown that helpers can buffer detrimental effects of unfavourable environmental conditions on the breeding female, securing its fecundity (Groenewoud & Clutton-Brock, 2021; Wiley & Ridley, 2016). Similarly, it is possible that helpers also buffer the reductions in pup care by pregnant females, however, further analysis will be needed to substantiate that.

We also found that pregnancy effects largely explained the differences between dominant and subordinate females in contributions to pup provisioning and sentinel guarding, though not to babysitting (discussed below). Clutton-Brock et al. (2004) first reported reduced cooperative behaviour in dominant meerkats, and suggested that this stems from their need to conserve body condition for future reproduction as opposed to subordinates that are less likely to breed. Our findings support this explanation and suggest that the explicit mechanism is gestation costs overlapping with nurturing dependent young, which is much more frequent in dominants.

In many other cooperative breeders, pregnancy rates are much higher in dominant females than in subordinates (Bennett & Faulkes, 2000; Koenig & Dickinson, 2016), so this may explain differences in cooperative behaviour between dominants and subordinates also in other cooperative breeding species. For example, in naked and Damaraland mole-rats, dominant breeding females contribute less to cooperative activities than subordinate



females (Houslay et al., 2020; Lacey & Sherman, 1991). Like morphological differences between them (Thorley et al., 2018; Young & Bennett, 2010), both are sometimes considered as the result of contrasts in early development, analogous to incipient caste systems found in some eusocial insects (Alexander et al., 1991; Jarvis & Bennett, 1993; Scantlebury et al., 2006). However, these morphological differences usually appear only after the acquisition of dominant breeding status (Johnston et al., 2021; Thorley et al., 2018), indicating an important difference from insect castes. Also in meerkats, no behavioural divergence in cooperative behaviour, including babysitting, was found prior to acquiring dominance role (Carter et al., 2014; Clutton-Brock et al., 2003), but only following it (Carter et al., 2014; Clutton-Brock et al., 2001, 2004; Huchard et al., 2016).

Babysitting by dominants was the only behaviour that was unaffected by pregnancy status since dominant females seldom babysit whether or not they are pregnant (babysitting probability: 2%). As a result, pregnancy did not explain the large difference in babysitting frequency between dominants and subordinates. This raises the question why dominant females hardly ever contribute to babysitting. One possible explanation is that babysitting, which involves foregoing foraging with the group for a half or full day at a time and is the most demanding cooperative behaviour (Clutton-Brock et al., 1998; Russell et al., 2003), would hamper the capacity of dominants to control their group. While apart from the group, dominant females cannot engage in dominance assertions to maintain hierarchy (Duncan et al., 2018) or in evictions of adult females to monopolize reproduction (Clutton-Brock et al., 2001; Young et al., 2006). Thus, hampering the need to secure dominance could be what distinguishes dominants babysitting behaviour to be both rare and unaffected by pregnancy status.

Pregnancy effects not explaining the large differences between dominants and subordinates in babysitting, and only explaining provisioning and guarding differences, raises the question whether pregnancies explain a biologically significant part of the cooperation differences between dominants and subordinates. Over a single reproductive bout, subordinates babysit on average 4 days and dominants do not babysit (Clutton-Brock et al., 2004), generating a difference of 4 foraging days. Translating the provisioning and guarding differences to a currency of foraging time differences is not straightforward, but we approximate that they amount for 1 and 1.3 more days of foraging for the dominants respectively (see [Supporting Information Text](#) for approximation explanation). Thus, pregnancies might explain 36% of the differences in pup care investment between dominants and subordinates in terms of impact on foraging time (explained part: 2.3-day difference owing to provisioning and guarding differences; nonexplained part: 4-day difference owing to babysitting differences). Nonetheless, it is likely that pregnancies might explain even a larger portion in terms of impact on energy budget because provision and guarding are more active behaviours that probably require more energy expenditure than babysitting pups in the borrow. We believe that this pregnancy-related difference is biologically relevant particularly because meerkats occupy an arid habitat with unpredictable rainfall (Huchard

et al., 2016), wherein they occasionally suffer from low resource abundance, inducing population declines in body weights and survival (Paniw et al., 2019). Under such conditions, even moderate changes in cooperative workload could result in significant short-term growth costs (Russell et al., 2003), and meerkats finely adjust their cooperative contributions in response to changes in resources or climate (Rauber et al., 2019; Russell et al., 2003).

The relationship between pregnancy and reductions in contributions to pup care may be influenced by some unmeasured variables such as the lactating frequency and quantity. In horses, lactating mothers that are concurrently at early stages of pregnancy wean their foals earlier than lactating mothers that are not pregnant (Cameron et al., 2000; Duncan et al., 1984), yet lactating-pregnant mothers lactate their foals for longer suckling bouts than nonpregnant mothers (Bartosova et al., 2011), possibly to prepare them for the earlier weaning. If a similar enhanced lactating pattern occurs also in early pregnant meerkats, this may foster the decrease in cooperative behaviour during the first half of pregnancy. However, since most lactating activity occurs in the natal borrow even before the pups first emergence, data on suckling bout frequency and duration were not available.

Reproductive overlap between pregnancy and rearing dependent young is not rare in mammals (e.g. Bartosova et al., 2011; Carrillo-Martinez et al., 2011; Dewsbury, 1990; Gilbert, 1984; Happold & Happold, 1990; Lee et al., 2019; Lucan et al., 2014; Mayor et al., 2006; Tardif et al., 2003; Trillmich & Wolf, 2008), and more research is needed to understand its occurrence and implications. We showed that pregnancy reduces investment in concurrent pup care in meerkats yet more research is needed in both cooperative and noncooperative breeding mammals to generalize these results, to explore the potential fitness consequences of this reproductive overlap, and to understand the determinants of its occurrence across mammal species.

## AUTHOR CONTRIBUTIONS

Shay Rotics and Tim Clutton-Brock conceived the study; Shay Rotics analysed the data and wrote the first draft; Frank Groenewoud consulted with the statistical analysis; Marta Manser and Tim Clutton-Brock contributed to managing the data collection and authors contributed to the manuscript by commenting on the drafts.

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#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gxd2547rf> (Rotics et al., 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Tables S1a–b.** Pregnancy status effects on individual relative contribution to pup provisioning - results of a GLMM and post-hoc comparisons.

**Tables S2a–b.** Pregnancy status effects on individual relative contribution to guarding - results of a GLMM and post-hoc comparisons.

**Table S3a–b.** Pregnancy status effects on babysitting- results of a GLMM and post-hoc comparisons.

**Table S4.** Pregnancy status effects on the proportion of food items that females donated to pups (generosity)- results of a GLMM.

**Table S5.** Changes throughout pregnancy days in relative individual contribution to provision modelled using GAMM.

**Table S6.** Changes throughout pregnancy days in body weight (g) modelled using GAMM.

**Table S7.** The effect of being pregnant while lactating (yes/no) on lactation duration - results of an LMM.

**Table S8.** Rank (dominant/subordinate) differences in the probability of being pregnant (yes/no) during the pup-provisioning period - results of a GLMM.

**Table S9.** Subordinates contraception experiment: comparisons of cooperative behaviours between subordinate females treated with contraceptive jab versus control subordinate females (saline jab).

**Table S10.** Pregnant females feeding experiment: comparisons of cooperative behaviours between late pregnant dominant females that were provided with food supplement versus control unfed dominant females.

**Table S11.** Pregnancy status effects on individual absolute contributions to provisioning and guarding - results of two separate GLMMs. This table summarizes the results of repeating the analyses conducted on relative contributions to provisioning and guarding (Tables S1 and S2) with analyses on absolute contributions.

**Figure S1.** Pregnancy effects on absolute contributions to cooperative behaviours. This figure is equivalent to Figure 1a,b in the manuscript but presents absolute contributions rather than relative ones.

**Figure S2.** Effects of pregnancy-related, experimental manipulations on individual absolute contributions to provisioning. This figure is equivalent to Figure 3 in the manuscript but presents absolute contributions rather than relative ones.

**Figure S3.** Differences between dominants (DOM) and subordinates (SUB) in cooperative behaviours (provisioning, guarding and babysitting) without accounting for pregnancy status.

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