

# Meerkat helpers buffer the detrimental effects of adverse environmental conditions on fecundity, growth and survival

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## Abstract

1. Recent comparative studies show that cooperative breeding is positively correlated with harsh and unpredictable environments and it is suggested that this association occurs because helpers buffer the negative effects of adverse ecological conditions on fitness.
2. In the Kalahari, rainfall varies widely between- and within years, affecting primary production and the availability of the principal prey of cooperatively breeding Kalahari meerkats, *Suricata suricatta*. Our study aimed to establish whether the presence and number of helpers buffer the negative effects of variation in rainfall on the fecundity and body mass of breeding females, and the survival and growth of pups.
3. We investigate the relationship between group size and variation in rainfall on dominant female fecundity, body mass, and offspring survival and growth using an additive modelling approach on 21 years of individual-based records of the life histories of individual meerkats.
4. We show that breeding female fecundity is reduced during periods of low rainfall but that the effects of low rainfall are mitigated by increases in group size and body mass because heavier females and those in larger groups have increased fecundity and reduced interbirth intervals. Pup growth and survival are also reduced during periods of low rainfall, but only in smaller groups.
5. Our results support the suggestion that cooperative breeding mitigates the detrimental effects of adverse environmental conditions and may enhance the capacity of species to occupy environments where food availability is low and unpredictable.

**Keywords:** cooperative breeding, environmental conditions, fecundity, group size, growth, meerkat, offspring survival, *Suricata suricatta*

## 1 INTRODUCTION

Recent comparative studies of birds and mammals have shown that, on a global scale, cooperative breeding is positively correlated with harsh and unpredictable environments (Cornwallis et al., 2017; Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017a) and it has been suggested that this is because cooperative breeding improves fecundity in breeding females as well as the growth and survival of their offspring under

unfavourable conditions, buffering the negative impacts of environmental fluctuations on fitness (Emlen, 1982; Hannon et al., 1987). In arid environments, both variation in rainfall and in temperature can have substantial effects on fecundity and survival (Gilmore & Cook, 1981). For instance, years of low rainfall substantially delayed the onset of reproduction and reduced birth rates in six species of African ungulates (Ogutu et al., 2013) and high ambient temperatures have been shown to lead to reduced reproductive success in two cooperative breeders: pied babblers *Turdoides bicolor* (Wiley & Ridley, 2016) and African wild dogs *Lycaon pictus* (Woodroffe et al., 2017).

The presence and number of helpers in cooperative breeding groups can affect female fecundity and offspring survival in several ways. First, members of larger groups may be more efficient in obtaining food, either through cooperative hunting or foraging or through their ability to defend larger and better territories, and dominant females in such groups might show improved body condition and fecundity (Dyble et al., 2019; Krause & Ruxton, 2002). In addition, helpers can also reduce female workload during the offspring rearing period ('load lightening'), thereby improving the body mass, interbirth intervals and breeding frequency of breeding females (Guindre-Parker & Rubenstein, 2018; Hatchwell, 1999; Lukas & Clutton-Brock, 2012). The total amount of food provided to offspring also increases in larger groups, and improvements in offspring growth are particularly important when food is scarce and starvation is a common cause of offspring mortality (Hatchwell, 1999). However, living in a larger group can also increase competition for food, especially when environmental conditions are poor and food availability is low, potentially resulting in reductions in female fecundity, offspring growth and survival (Bateman et al., 2012; Hoogland, 1995; Ozgul et al., 2014). The ability of groups to improve reproductive success under poor breeding conditions will therefore depend on how relationships between fecundity, offspring survival and group size change with environmental conditions and food availability.

There is growing evidence that helper number can modify the effects of variation in rainfall and temperature on fecundity, offspring growth and survival in cooperative breeders. For example, in azure-winged magpies *Cyanopica cyanus*, the presence of helpers improved provisioning rates to a greater extent when high rainfall during the breeding season decreased insect availability (Canario et al., 2004) and, in sociable weavers *Philetairus socius*, the fledgling mass of pairs without helpers was more affected by low rainfall than that of pairs with helpers (Covas et al., 2008). A long-term study of cooperative breeding superb starlings *Lamprotornis superbus* showed that females living in larger groups gained increased reproductive success and reduced workload under both adverse and benign conditions, while males only benefit in the latter (Guindre-Parker & Rubenstein, 2018). However, some studies have produced contrary results: for example, a long-term study of acorn woodpeckers showed that (male) helpers had a positive effect on breeder fecundity and adult survival in good, rather than poor acorn years, suggesting that the positive effects of group size are greater in larger groups under beneficial conditions and are reduced when conditions are harsh (Koenig et al., 2011).

Here we use a 21-year study of wild Kalahari meerkats *Suricata suricatta* to investigate how variation in rainfall and group size interact in their effects on fecundity, offspring growth and survival and to assess whether relationships between groups size and the reproductive success of breeding females occur because helper number has a positive influence on female body mass. Meerkats are obligate cooperative breeders with groups consisting of a dominant breeding pair and a variable number of subordinates that all engage in alloparental care

including the provisioning and defence of young (Russell, Clutton-Brock, et al., 2002; Santema & Clutton-Brock, 2013). The southern Kalahari is characterised by seasonal rains that usually start in October, reach their peak in January and can last until April (Doolan & Macdonald, 1996a). Both the timing and extent of rainfall vary between years: for example, between 1998 and 2019 total annual rainfall varied from 133 mm to 460 mm and the percentage that fell in the first half of the year versus the second half of the year from 38.3% to 88.1%, though there has been no obvious trend in annual rainfall in the region over the last 21 years (F. Groenewoud & T. H. Clutton-Brock, in prep). Variation in rainfall is strongly correlated with the availability of the prey items upon which meerkats feed, mostly grubs, larvae, insects, arachnids scorpions and lizards (Doolan & Macdonald, 1996a; Scantlebury et al., 2004). Previous work on this study population has shown that both rainfall and group are important predictors of dominant female fecundity, pup growth and survival (Clutton-Brock et al., 1999; Hodge et al., 2008; Russell, Brotherton, et al., 2003): mean annual number of litters produced per group decreased from more than three in years with high rainfall (>300 mm) to fewer than one in years where rainfall was low (<100 mm; Clutton-Brock et al., 1999) and body mass—an important predictor of dominant female fecundity—is negatively affected by reductions in rainfall (Ozgul et al., 2014; Paniw et al., 2019). It is currently unclear, however, to what extent the relationship between rainfall, body mass, fecundity and pup survival are dependent on group size, potentially enabling larger groups to buffer the negative effects of adverse conditions on fitness.

Our analysis asks four groups of questions: (a) what is the relationship between rainfall and fecundity and is this relationship modified by group size and female body mass? (b) What is the relationship between rainfall and dominant female body mass and is this relationship modified by group size? (c) What are the relationships between rainfall, pup growth, pup survival, and are these relationships modified by group size? and (d) are positive effects of group size on female breeding success a consequence of reductions in the costs of breeding to females resulting in improvements in their body mass in years when food availability is low? Our dataset spans 21 years (1998–2019) during which the reproductive attempts of all females in our 50–60 km<sup>2</sup> study area have been monitored, group compositions were recorded at least weekly and we collected regular records of individual weights. This provides us with unusual opportunities for investigating the effects of group size on fecundity and offspring survival under contrasting environmental conditions.

## 2 MATERIALS AND METHODS

### 2.1 Study species

We monitored the body mass and breeding success of 168 dominant females and the growth and survival of 2,127 individually marked meerkat pups from 500 litters belonging to 89 different social groups from July 1998 until July 2019 at the Kuruman River Reserve (26°58'S, 21°49'E) in the Northern Cape, South Africa. Meerkats are small ( $M \pm SD = 661 \pm 83$  g for individuals older than 1 year of age) cooperative breeding vertebrates that live in social groups that typically consist of a pair of unrelated breeding adults (dominants) and up to 40 non-breeders (subordinates) of either sex and of different ages that are mostly the offspring of the dominant breeding female or of previous dominant females in the same group. In the current study, groups contained on average  $11.7 \pm 7.3$  ( $M \pm SD$ ; range = 1–38) individuals over 6 months of age of which 47.5% were female (89 groups, 3,759 'group months'). Subordinate females are typically evicted from their natal group by the resident dominant females between the ages of 2 and 4 years, while subordinate

males leave their natal groups voluntarily between the ages of 2 and 5 years (Clutton-Brock et al., 2001; Clutton-Brock & Manser, 2016; Maag et al., 2018).

Females can breed throughout the year, but reproduction is substantially lower during the dry winter months (April–September) compared to summer (October–March) when most rainfall occurs (Mares et al., 2014; Figure 2). A typical dominant female litter consists of four pups (range = 1–7;  $M \pm SD = 3.59 \pm 1.32$ ;  $N = 738$  litters) and dominant females can produce up to four litters each year (range = 0–4,  $M = 1.18$ ). Most subordinate females do not breed though older individuals occasionally do so (Clutton-Brock et al., 2001). Pups are born underground and typically emerge from the burrow between 3 and 4 weeks of age and are subsequently fed by all group members until they are approximately 3 months old (Brotherton, 2001). In addition to providing food to pups, subordinates engage in cooperative tasks such as anti-predator behaviours and allolactation—females only (Clutton-Brock et al., 2002).

Almost all meerkats in our study population are individually marked from birth and habituated to close observation (Clutton-Brock & Manser, 2016). Groups are visited in the morning and afternoon every 1–3 days during which any changes in group composition through births, deaths, evictions and immigrations are recorded. Individuals are weighed in the morning, just after leaving their burrow, by standing on a digital scale in return for a small reward of food (usually boiled egg) or water. We identified the presence of individuals in each group on a monthly basis and quantified monthly group size in our study as all individuals over 6 months of age which is the time at which subordinates start showing cooperative behaviours (Clutton-Brock et al., 2002). Individuals that disappeared from their groups before 6 months of age were assumed dead, since dispersal before this age has never been observed (Clutton-Brock et al., 2002; Doolan & Macdonald, 1996b).

## 2.2 Rainfall

We obtained monthly rainfall data for our location from 1979 to 2019 from the National Oceanic and Atmospheric Administration (NOAA) using the version 2.3 combined Global Precipitation Climatology Project (GPCP) dataset which integrates data from rain gauge stations and satellites to estimate monthly rainfall on a 2.5 degree global grid (Adler et al., 2013; see <https://psl.noaa.gov/> for more information). We validated this data by comparing it to rainfall collected at our field site (2009–2019), and correlations showed high agreement ( $R^2 = 0.74$ ) between the two measures (see Supporting Information).

We calculated standardised measures of rainfall (standardised precipitation index or ‘SPI’; Mckee et al., 1993) on a 1-, 3-, 6- and 12-month time-scale using 40 years of monthly historical rainfall data and the methods advocated in Stagge et al. (2015) using the sci package v1.0-2. Previous studies in our population have used standardised measures of rainfall in the form of z-scores (Ozgul et al., 2014; Paniw et al., 2019), which are similar to the SPI, and we expand on our choice for the SPI as well as its characteristics in relation to z-scores in the Supporting Information. Briefly, the SPI is a well-reviewed meteorological drought index that can assess drought severity across regions with varied climatic and hydrologic regimes. The SPI fits rainfall to a predefined probability density function and transforms it to a standard normal distribution ( $\mu = 0$ ,  $\sigma^2 = 1$ ) where values represent deviations from monthly or accumulated monthly means (Mckee et al., 1993). This offers two major advantages over using raw measures of rainfall: (a) decoupling the covariance between season and rainfall into a separate seasonal and rainfall component, allows us to estimate the effect of (surplus or deficit) rainfall independently from consistent seasonal effects, which is

likely a better indication of environmental harshness than raw rainfall data alone; (b) the possibility of using accumulated monthly means enables us to investigate the additive effect of variation in rainfall over longer time periods and (c) the SPI is directly related to probability and any long-term climate record will spend approximately 9.2% of time in moderate drought conditions (SPI = -1.00 to -1.49), 4.4% of time in severe drought conditions (SPI = -1.50 to -1.99) and 2.3% in extreme drought conditions (SPI  $\leq$  -2.00; Mckee et al., 1993). More information on the relationship between SPI and raw measures of rainfall in our study area is found in the Supporting Information. Due to the seasonal patterns of rainfall and reproduction in our study population, we defined the start and end of years as 1 July and 31 June, respectively (Doolan & Macdonald, 1996a).

### 2.3 Body mass

To reduce bias due to measurement error, we estimated daily individual body mass by fitting log-transformed morning body mass in a linear mixed-effect model (LMM) assuming a Gaussian error structure using the nlme package v3.1-142. We added nested random intercept terms for *individual*, *year*, *month*, *day* and *age in months*, and we added *sex* as a fixed effect. We then predicted an individual's mass for each day it was weighed and used these predictions as a measure of an individual's mass in further analyses. To avoid bias due to the increased body mass of dominant females during pregnancy, we excluded all measurements of body mass from the timing of conception until abortion or birth.

### 2.4 Statistical methods

#### 2.4.1 Fecundity

We expected the effects of seasonality, rainfall and group size on our variables of interest to be nonlinear since the benefits of group size and rainfall are likely to suffer from diminishing returns and such patterns have been found previously in our population (Ozgul et al., 2014; Paniw et al., 2019). We therefore constructed generalised additive mixed-effects models (GAMMs) to deal with these nonlinearities, without superimposing prior restrictions on the shape of the relationships. For all response variables investigated here, we fitted full models with 1-, 3-, 6- and 12-month SPI's and used AIC values to determine which time-scale best predicted our variable of interest. To analyse the fecundity of dominant females, we fitted the quarterly (July–September, October–December, January–March and April–June) number of pups emerging from the burrow as a response variable in a generalised additive mixed model (GAMM) using the mgcv package v1.8-31 (Wood, 2004, 2011). For this and all other models, we used cubic regression splines for continuous variables and cyclic cubic regression splines to model seasonality, that is, *quarter* or *month*. Fecundity showed signs of being zero-inflated: births for individual females were restricted to only a few quarters of the year, and subsequent litter sizes were relatively large, violating the Poisson mean-variance relationship. We therefore estimated fecundity by fitting zero-inflated Poisson models, with separate linear predictors for the logistic and Poisson part of the model. This approach further enabled us to infer whether covariates influenced the number of offspring produced (i.e. litter size), or the likelihood of reproduction (i.e. breeding frequency). We fitted a three-way tensor product interaction containing *group size*, *SPI* and *quarter*, and all underlying two-way tensor product interactions and main effects as predictors. Although three-way interactions can be interpreted in multiple directions, one useful way of thinking about this three-way tensor product interaction in particular is that it posits the hypothesis that the correlation between group size and fecundity depends on rainfall and that the strength of this relationship is

conditional on season. While group size and SPI are always modelled as continuous predictors in tensor product smooths, we sometimes describe or visualise such interactions by holding one of these variables at a fixed value, that is, high (1.5) or low (-1.5) for SPI, and small (3), medium (11) or large (26) for group size. We also included smooths for *age in months* and for average population group size which is highly correlated to population density (Bateman et al., 2013; hereafter *population density*). We included random intercepts for *individuals*. We also determined the relative importance of *group size* and *SPI*, and the interaction between these on fecundity by estimating the percentage of deviance explained by each term as well as the differences in AIC values between models with and without these terms.

To assess the extent to which the relationship between *group size*, *SPI* and fecundity was mediated by body mass, we fitted an additional model where we included the quarterly body mass of dominant females and determined (a) the relative deviance explained by body mass and (b) the relative deviance explained by group size, rainfall and the interaction between these. If the relationship between group size, rainfall and fecundity was the result of increases in body mass, we would expect the relative deviance explained by group size and rainfall to decrease.

For model selection, we relied on an additional penalty to each term so that effects could be penalised to zero (Marra & Wood, 2011). The significance of smooth terms was assessed by Wald  $\chi^2$ -tests (Wood, 2013). We checked additive models for violations of model assumptions such as normality of residuals, heteroscedasticity and adequate selection of  $k$  (i.e. ‘wiggleness’). Model selection and inference as described here was applied to all subsequent additive models. All analyses presented were performed in R 3.5.1 (R Core Team, 2016).

#### **2.4.2 Dominant female body mass**

We estimated how dominant female body mass changed with rainfall in groups of varying sizes by fitting average quarterly body mass as a response variable in a GAMM with a Gaussian error distribution. We used a quarterly measure to ensure that we had sufficient body mass data for each time step in our model, even in the case of female pregnancies. We included a three-way tensor product interaction for *group size*, *SPI* and *quarter*, and all underlying two-way tensor product interactions and smooths as predictors. We also included random intercepts for *individuals*, and smooths for *age in months* and *population density*.

#### **2.4.3 Costs of reproduction and inter-litter intervals**

As an additional investigation into the causes of variation in dominant female fecundity, we assessed whether dominant females lost weight over the course of the breeding season as a result of reproduction, whether weight loss increased with litter number and whether dominant females in larger groups showed reduced weight loss. We fitted dominant female growth to the next month in a linear mixed model with *month*, *year* and *individual* as random effects to account for seasonal effects and the repeated measurement of the same individuals over time, respectively. We included monthly *body mass*, *SPI*, *group size* and whether individuals reproduced that month as a 0–1 event as predictors, as well as the two-way interaction between the latter and *group size* and *rainfall*. We dropped variables from the model, starting with interactions if this resulted in a model with a lower AIC value. Parameter inference was based on log-likelihood ratio tests of nested models assuming a  $\chi^2$ -distribution.

To test whether weight loss increased with litter number, we fitted a second model where we removed the binary predictor variable indicating whether individuals had reproduced and included litter number as a predictor instead.

We also tested how inter-litter intervals changed with *body mass* and *group size*. We fitted interbirth interval (time to the birth of the next litter in days) as a response variable in a linear mixed-effects model with *Year* as a random effect and we included *SPI*, *group size*, *body mass* and *dominant female age* as predictors. We also included a second-order polynomial for dominant female age to account for any nonlinear effects of age on fecundity and litter number as a predictor in this model.

#### **2.4.4 Survival**

We analysed the monthly survival of pups from emergence to nutritional independence (90 days) by fitting survival to the next month (1 = yes, 0 = no) as a response variable in a GAM with a logit link function. We only included pups with known birthdates. Most individuals in this dataset that had died before 90 days of age ( $N = 505$  out of 2,127 individuals; 23.7%) either disappeared ( $N = 445$ ; 88.1%), were found dead ( $N = 51$ ; 10.1%) or were known to be predated ( $N = 6$ ; 1.2%). Three individuals were euthanised for animal welfare purposes but were included since they would likely have died natural deaths shortly after. We fitted a three-way tensor product interaction for *group size*, *SPI* and *age in days*, and all underlying two-way tensor product interactions and smooths as predictors. We also included a tensor product interaction containing *SPI* and *month*, to account for seasonal differences in the effect of rainfall on pup survival.

#### **2.4.5 Pup growth**

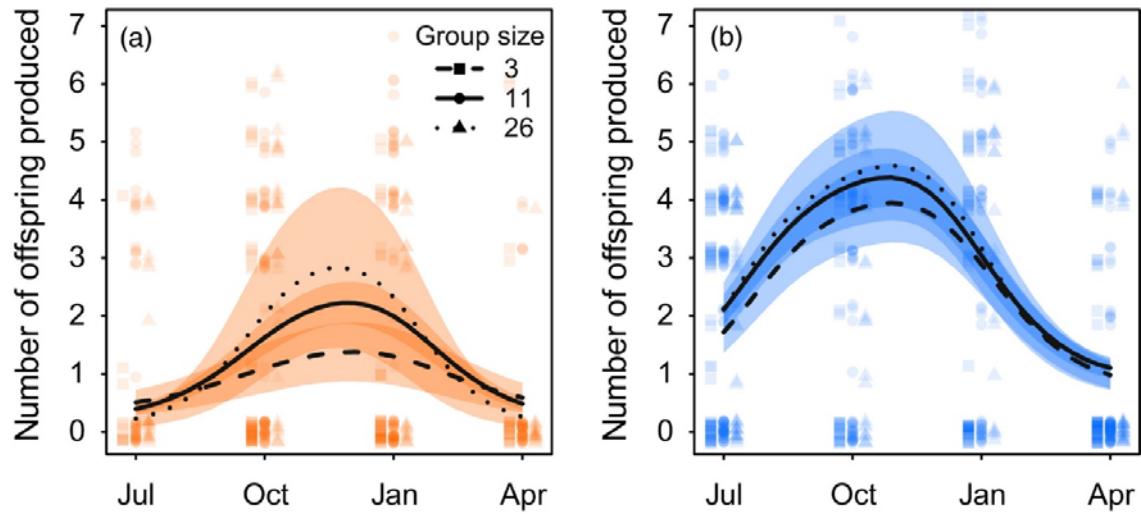
To investigate whether group size buffered the negative effects of low rainfall on offspring growth, we fitted the monthly body mass of offspring from emergence to 3 months of age as a response variable in an additive mixed model with a Gaussian error distribution. We included a three-way tensor product interaction for *group size*, *SPI* and *age in days*, and all underlying two-way tensor product interactions and smooths as predictors. We also included smooths for the *number of litter mates*, *month* and *population density*, as well as a tensor product interaction between *number of litter mates* and *age in days*. We included random intercepts for *litters* to account for similarities in body mass between pups from the same litter.

### **3 RESULTS**

#### **3.1 Female fecundity**

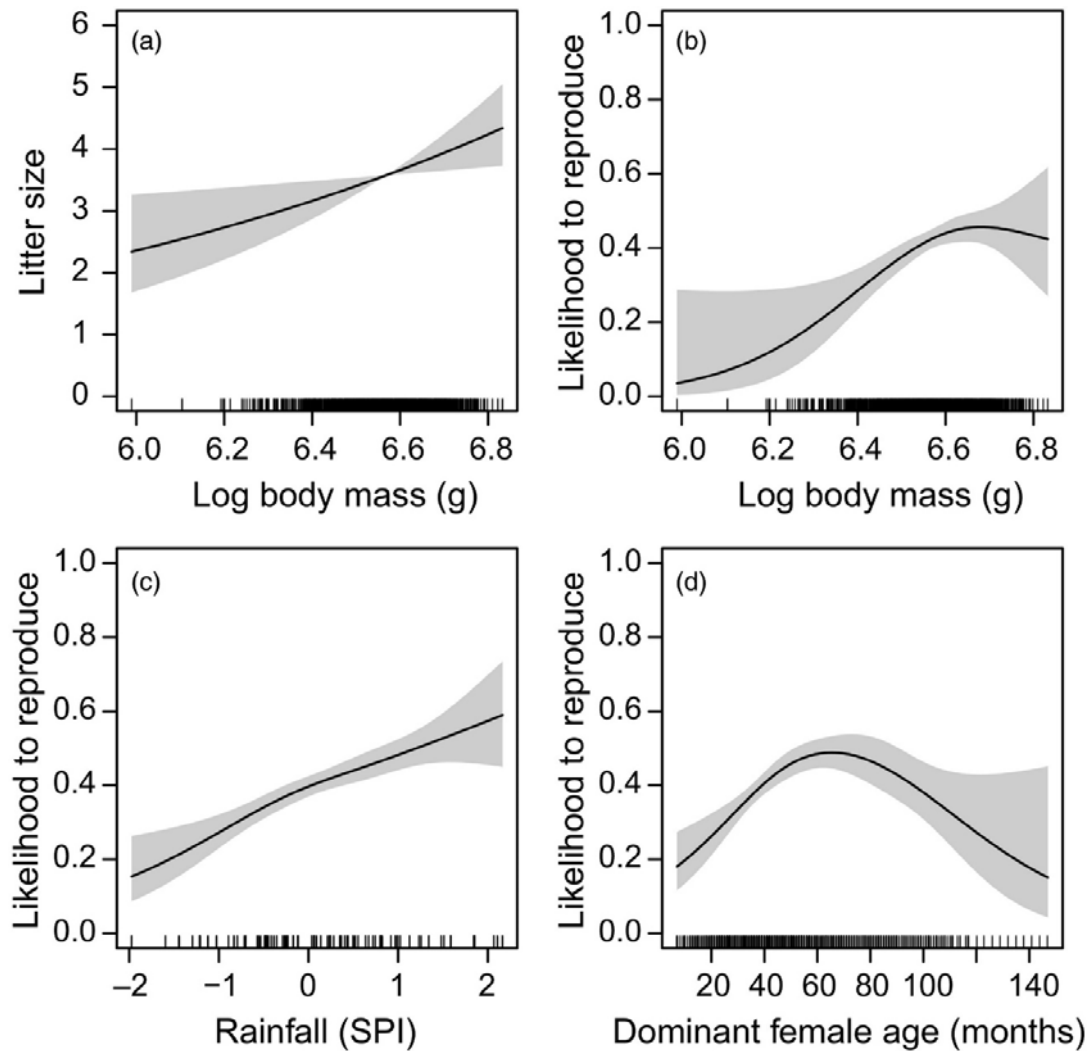
The fecundity of dominant females increased with SPI as a result of increases in breeding frequency rather than increases in litter size (Figures 1 and 2; Table S1) and higher SPI was associated with an increased likelihood of breeding early in the season (Figure 1). Dominant female fecundity also increased with group size as a result of increases in breeding frequency rather than litter size, but this relationship was constrained to the early and middle breeding season and there was no relationship between group size and fecundity during other periods of the year (Figure 1; Table S1). Female birth rates initially increased with age but declined from 6 year of age onwards (Figure S1; Table S1). There were no significant relationships

between litter size and SPI or group size, but litter sizes were largest in January compared to other periods of the breeding season (Table S1).



**Figure 1.** The quarterly fecundity (number of pups produced) of 168 dominant female meerkats from 1998 to 2019 during (a) low and (b) high rainfall conditions for small (dashed lines), medium (solid lines) and large (dotted lines) group of meerkats representing the 5%, 50% and 95% percentiles in group size, respectively. Errors are based on 95% CI and symbols indicate different subsets of raw values for low (SPI < 0) and high (SPI > 0) rainfall conditions. Rainfall was modelled continuously but for visualisation purposes we chose to plot the effects for SPI =  $-1.5\sigma$  (moderately dry) and SPI =  $+1.5\sigma$  (moderately wet) for low and high rainfall, respectively



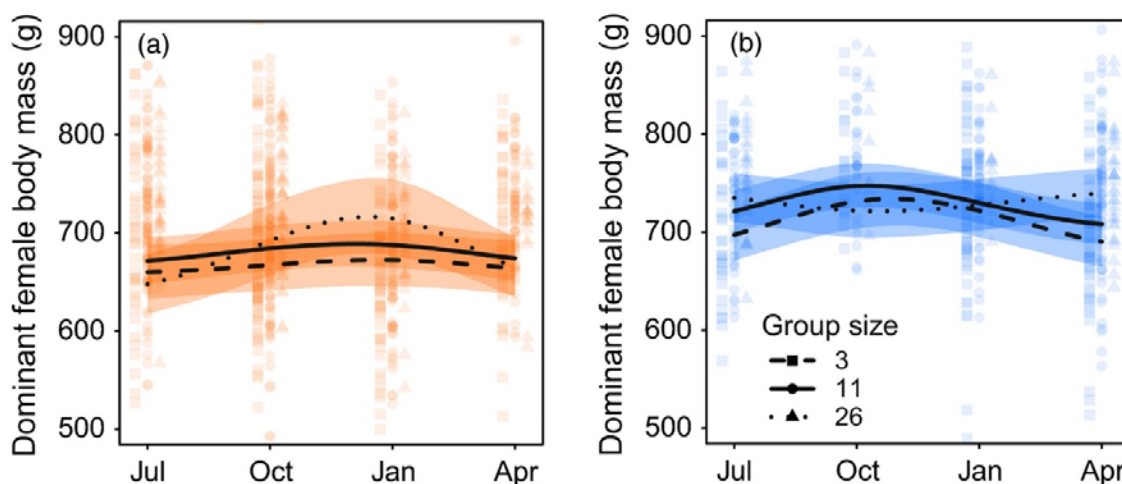


**Figure 2.** Component smooth effects of (a) dominant female body mass on litter size and (b) dominant female body mass, (c) rainfall and (d) dominant female age on the likelihood that dominant female meerkats produce a litter. Lines and shaded regions indicate mean predicted values and standard errors, and vertical ticks at the bottom of each graph give an indication of data density

Standardised precipitation index and group size accounted for 4.6% and 1.2% of total model deviance before the inclusion of dominant female body mass to the model investigating dominant female fecundity. When we included dominant female body mass to this model, the deviance explained by SPI and group size decreased by 1.2% and 0.2%, respectively, indicating that the relationship between SPI, group size and dominant female fecundity was partly mediated through body mass. Dominant female body mass was positively correlated with dominant female fecundity: heavier females gave birth to larger litters and had higher birth rates (Figure 2; Table S1). The relationships between group size and SPI and the likelihood that dominant females would give birth remained significant despite the inclusion of dominant female body mass in the model, which is a further indication that these relationships are additive.

### 3.2 Dominant female body mass

Dominant female body mass increased with age until 5–6 years of age and declined thereafter and also declined with increasing population density (Table S2; Figure S1). There was an overall positive relationship between SPI and dominant female body mass and average female weight ranged from 747 g in wet conditions ( $SPI = +1.5\sigma$ ) to 648 g in dry conditions ( $SPI = -1.5\sigma$ ). Variation in rainfall also changed the dynamics of dominant female body mass: under dry conditions (low SPI), female body mass increased in the first two quarters (July–December), peaking in the third quarter (January–March) while, under wet conditions (high SPI), body mass was highest in October to November and declined thereafter (Figure 3; Figure S1; Table S2). Group size modified both these effects: under dry conditions, dominant females in larger groups increased in body mass more than dominant females in smaller groups. However, under wet conditions, dominant females in larger groups initially decreased in weight, reaching lowest body mass in October–December, while dominant females in smaller groups increased in weight and reached highest body mass during the same period (Figure 3; Table S2).



**Figure 3.** The quarterly body mass of 168 dominant female meerkats from 1998 to 2019 for (a) low and (b) high rainfall conditions as indicated by a 6-month accumulated standardised precipitation index (SPI). Lines indicate mean predicted values for small (dashed lines), medium (solid lines) and large groups (dotted lines) which represent the 5%, 50% and 95% percentiles in group size, respectively. Rainfall was modelled continuously but for visualisation purposes we chose to plot the effects for  $SPI = -1.5\sigma$  (moderately dry) and  $SPI = +1.5\sigma$  (moderately wet) for low and high rainfall, respectively

### 3.3 Costs of reproduction and inter-litter intervals

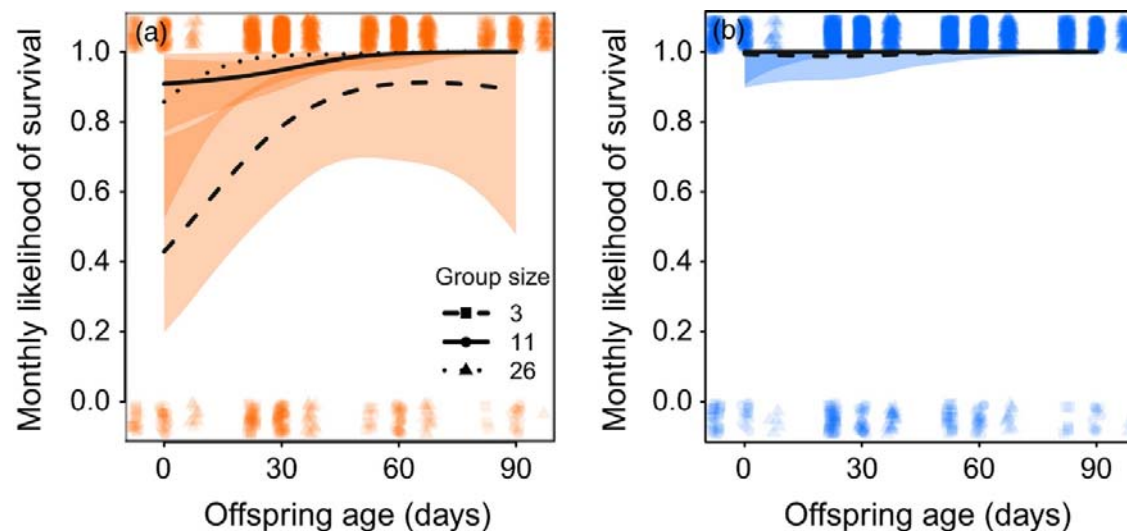
Dominant females lost more body mass in the months where they reproduced compared to months where they did not and this relationship was modified by rainfall: dominant female weight gain increased more with SPI when they did not produce litters than when they did (Figure S2;  $SPI * \text{reproduced}: M \pm SE = -5.47 + 2.34, df = 1, \chi^2 = 5.48, p = 0.02$ ). Group size also improved dominant female monthly weight gain ( $M \pm SE = 0.40 + 0.17, df = 1, \chi^2 = 5.90, p = 0.02$ ), but this relationship was independent of whether females reproduced that month or not (group size \* reproduced:  $M \pm SE = -0.087 \pm 0.12, df = 1, \chi^2 = 0.53, p = 0.47$ ). There was also no indication that dominant female weight loss differed between litters ( $df = 1, \chi^2 = 0.04, p = 1.00$ ), or that the relationship between group size and dominant female weight loss, or

rainfall and dominant female weight loss changed with litter number. ( $\chi^2 = 0.35, p = 0.95, \chi^2 = 3.61, p = 0.31$ , respectively).

Group size and body mass reduced the time to a dominant female's next litter (group size:  $M = SE = -0.96 + 0.41, df = 1, \chi^2 = 5.35, p = 0.02$ ; body mass:  $M \pm SE = -68.28 \pm 30.08, df = 1, \chi^2 = 5.18, p = 0.02$ ), but there was no relationship between dominant female age or SPI and inter-litter interval ( $df = 2, \chi^2 = 1.52, p = 0.47$ ;  $df = 1, \chi^2 = 0.36, p = 0.55$ , respectively), and inter-litter intervals did not differ between subsequent litters ( $df = 2, \chi^2 = 4.14, p = 0.13$ ).

### 3.4 Pup survival

Pup survival was positively correlated with SPI, but this relationship was highly nonlinear and reductions in survival were restricted to low dry conditions ( $SPI < -0.5$ ): the survival of pups was uniformly high and mostly unaffected by changes in SPI for higher SPI values (Figure 4; Figure S3; Table S3). Pup survival was lowest just after emergence and shortly thereafter, until  $\sim 40$  days of age, and pups reared in small groups had lower survival during this period than those reared in large- or medium-sized groups (Figure 4; Table S3). Under good rainfall conditions, pup survival was largely unaffected by group size.

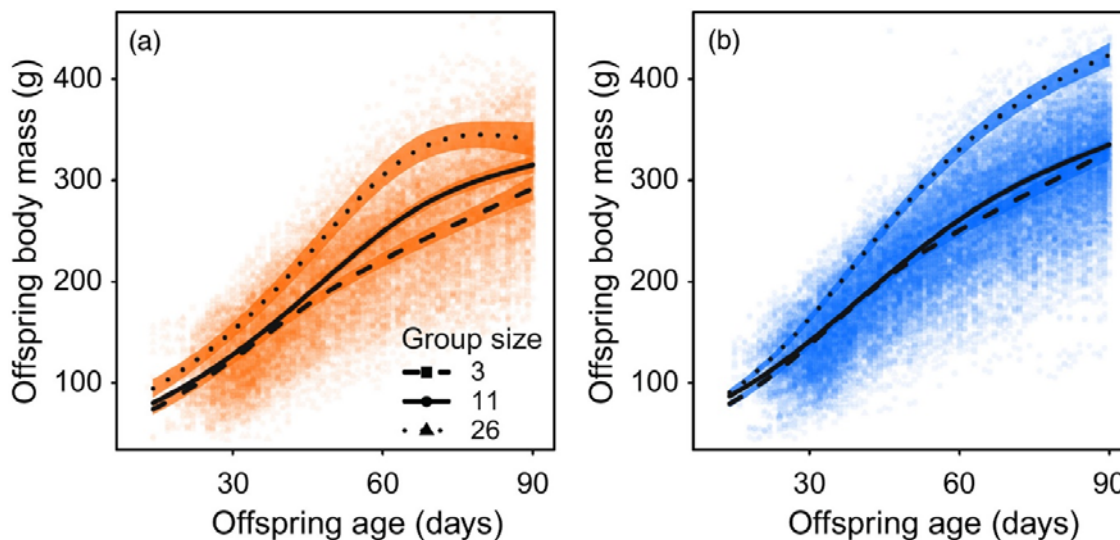


**Figure 4.** The mean predicted monthly survival of meerkat offspring from emergence to nutritional independence (90 days) during (a) low and (b) high rainfall conditions for small (dashed lines), medium (solid lines) and large groups (dotted lines). Errors are based on 95% CI and symbols indicate different subsets of raw values for low ( $SPI < 0$ ) and high ( $SPI > 0$ ) rainfall conditions. Rainfall was modelled continuously but for plotting purposes we chose to plot the effects for  $SPI = -1.5\sigma$  (moderately dry) and  $SPI = +1.5\sigma$  (moderately wet) for low and high rainfall, respectively

### 3.5 Pup growth

SPI had an overall positive effect on pup growth and here too, the relationship varied with group size (Figure 5; Figure S4; Table S4). During dry conditions, pup growth was initially similar for all group sizes, but pups in large or average groups showed higher growth after 40 days of age, compared to small groups (Figure 5). Pups in large groups showed reduced growth during dry conditions compared to wet conditions as they approached nutritional independence. However, these pups still reached higher body mass at 90 days of age than

pups reared under similar conditions in small groups (Figure 5). Under wet conditions, pup growth was initially similar for all group sizes, but pup growth after 40 days of age was positively related to group size and these differences persisted until pups were nutritionally independent at 90 days (Figure 5). Body mass of pups also decreased with an increasing number of litter mates and was highest during periods of average population density (Figure S4; Table S4).



**Figure 5.** Meerkat offspring growth from emergence to nutritional independence (90 days) under (a) low and (b) high rainfall conditions for small (dashed lines), medium (solid lines) and large groups (dotted lines). Errors are based on 95% CI and symbols indicate different subsets of raw values for low (SPI < 0) and high (SPI > 0) rainfall conditions. Rainfall was modelled continuously but for visualisation purposes we chose to plot the effects for SPI =  $-1.5\sigma$  (moderately dry) and SPI =  $+1.5\sigma$  (moderately wet for low and high rainfall, respectively)

#### 4 DISCUSSION

We show that reductions in rainfall (SPI) are associated with lower breeding frequency and body mass of dominant female meerkats, and that pup survival and growth were similarly depressed. Positive correlations between rainfall and breeding success are common in other species, including cooperative breeders (e.g. Curry & Grant, 1990; Mares et al., 2017), and these correlations are often likely to be a result of close associations between rainfall and food availability, especially in species living in arid habitats like the Kalahari (Churkina & Running, 1998; Doolan & Macdonald, 1996a). Several other studies, including those of Woodroffe et al. (2017) in wild dogs, Wiley and Ridley (2016) in pied babblers and van de Ven et al. (2019) in meerkats have also shown adverse effects of temperature variation on aspects of reproduction, similar to those of rainfall. However, rainfall is more variable than temperature both within- and between years and is more closely associated with variation in vital rates and fluctuations in population density (Ozgul et al., 2014; Paniw et al., 2019). Although these earlier studies found positive correlations between rainfall and aspects of fitness, Hodge et al. (2008), who used raw measures of rainfall (which can confound seasonal and rainfall effects), found no relationship between rainfall and birth rate, litter size or litter survival. The relationship between low rainfall and reduced fecundity in our study was mostly due to females having a reduced likelihood of giving birth, particularly during the early breeding season, resulting in shorter breeding seasons, but not because of changes in litter size (Figure 1). This suggests that either females do not conceive when rainfall is low

or, conceive but fail to carry their litter to term. It is likely that reduced rainfall—particularly early in the breeding season—reduces body mass and the number of litters that dominant females can rear each year (Paniw et al., 2019). Similarly, a recent study of sociable weavers *Philetairus socius* has found that early rainfall improves the number of clutches produced, while total rainfall is related to fledgling success, which also suggests that the timing of rainfall and its effect on breeding phenology is an important determinant of reproductive success (Mares et al., 2017; Visser & Gienapp, 2019).

Like previous studies of meerkats (Russell, Clutton-Brock, et al., 2002; Sharp & Clutton-brock, 2010), we found that pup survival was lower during low rainfall conditions, particularly during the time just after pups had emerged from the burrow (Figure 4; Figure S3). Increased pup mortality during droughts could have several causes, including starvation as a result of reduced pup provisioning, the group abandoning the pups when conditions deteriorate, increased predation or a combination of these. Our results show that survival is lowest just after emergence when pups are still relatively immobile, and not during the period when they are fed most by subordinates (Brotherton, 2001), which seems to suggest that increased predation or pups being abandoned are the most likely explanations.

Earlier investigations of the relationship between rainfall and pup growth in our population have produced contrasting results: across a smaller number of years, Russell, Clutton-Brock, et al. (2002) found no relationship between rainfall and pup daily growth rate or percentage daily weight gain while van de Ven et al. (2019) found a negative relationship between pup daily weight gain and rainfall 2 months prior. However, English et al. (2014) found that rainfall in the preceding 2 months was positively correlated to the monthly growth of dependent pups, and similarly, our study shows that offspring growth was depressed when rainfall was low (Figure 5; Figure S4). There are two main explanations for why our results and those of English et al. (2014) differ from these other studies. First, our study and that of English et al. (2014) account for seasonal differences in the growth of pups, thereby avoiding confounding the effects of rainfall with seasonal effects on pup growth. Second, our analysis and that of English et al. (2014) use changes in morning body mass over time, which is less variable and a better indicator of growth than daily weight gain since it is (a) less affected by daily variation in foraging success and prey water content and (b) also accounts for variation in nightly weight change. The discrepancy between these studies also suggests that pup weight gain over shorter periods might not reflect long-term growth and future studies would do well to test such assumptions explicitly.

Group size was positively correlated to the improved fecundity of dominant females mainly by an increased likelihood that they would give birth, but this relationship was restricted to the early- to middle breeding season (Figure 1). A subsequent analysis shows that group size and dominant female body mass—which is also higher in larger groups—are related to shorter interbirth intervals (Russell, Brotherton, et al., 2002). Body mass also increased the overall likelihood that dominant females would give birth, independent of seasonal effects, and was one of the few significant predictors of litter size, which further increased dominant female fecundity, consistent with previous meerkat studies (Russell, Brotherton, et al., 2002, 2003). Dominant females showed seasonal changes in body mass, and these body mass dynamics were differentially affected by SPI and group size (Figure 3; Figure S1). In small- and medium-sized groups, dominant females are overall heavier during high rainfall than low rainfall conditions, particularly during the breeding season, when most reproduction occurs. Dominant females in larger groups gained more body mass during the breeding season, but only when SPI was low rather than high. Our analyses investigating the monthly weight gain

of dominant females show that while dominant females in larger groups lose less body mass than those in smaller groups, this relationship is not stronger during dry conditions. When SPI was high, dominant females in large groups, but not in medium-sized or small groups, lost body mass, and these females instead were heaviest at the beginning of the dry season (Figure 1b). It is likely that decreased dominant female body mass in large groups and under high rainfall conditions are the result of dominant females engaging in the costly suppression of subordinate females: the number of older female subordinates that will try to breed is higher in larger groups and subordinate females are more likely to breed when they are in better body condition, which is likely to be the case when breeding conditions are good (Clutton-Brock et al., 2008). Moreover, if reduced body mass was the result of feeding competition, we would expect this to occur in low, rather than high rainfall conditions. In some cases, increased reproductive competition between group members can lead to the counterintuitive result that reproductive success is higher under unfavourable than under favourable conditions, as has been shown in Taiwan yuhina's *Yuhina brunneiceps* (Shen et al., 2012).

Pup survival was higher in larger groups and this relationship was most apparent during low rainfall conditions and after pups had just emerged from the burrow, until 40 days of age (Figure 4). Helpers can improve the survival of pups in several ways, including by minimising the risk of predation and starvation, which are both likely to be higher during periods of low food availability (Anholt & Werner, 1998). Meerkats pups are particularly vulnerable after they have just emerged because they are dependent on adult group members to babysit them while the rest of the group is out foraging (Clutton-Brock et al., 2004). Babysitters are more likely to abandon litters when their own body condition becomes too low, which is more likely to happen during periods of low food availability and when there are fewer group members around to share babysitting duties (Russell, Sharpe, et al., 2003). Additionally, it is not uncommon for pups that have only recently joined the rest of the group during foraging trips to get separated from the rest of the group, especially when food availability is low and groups likely need to traverse longer distances to forage.

Group size modified the effects of SPI on growth but did so differentially under dry or wet conditions (Figure 5; Table S4). Under dry conditions, offspring in differently sized groups initially had similar growth rates, but growth in large and medium-sized groups increased after 40 days of age compared to small groups (Figure 5). Under wet conditions, pup growth was very similar for small- and medium-sized groups, but offspring reared in large groups showed higher growth still. Offspring growth declined when pups approached nutritional independence in dry conditions compared to wet conditions, particularly in large groups, indicating that pups might suffer from increased competition for food in larger groups when the rate with which they are fed decreases. This is consistent with previous results in our study population which have found positive associations between group size and pup growth when pups are nutritionally dependent (between 1 and 3 months of age), but not after this age (English et al., 2014). Variation in growth and body mass can have important fitness consequences later in life because pups that are heavier at nutritional independence are more likely to obtain dominance and as a result have higher lifetime reproductive success (Russell et al., 2007).

It has been widely assumed that the relationship between cooperative breeding and harsh and fluctuating environments occurs because cooperative breeding buffers the negative effects of adverse environmental conditions on dominant fitness (Emlen, 1982; Hannon et al., 1987; Rubenstein, 2011). However, there is currently little consensus on whether such conditions

favour the formation of groups, alloparental care or both, and explanations for cooperative breeding may differ between taxa and species (Griesser et al., 2017; Lukas & Clutton-Brock, 2017b). In meerkats, subordinates living in larger groups gain direct benefits from increased survival (Clutton-Brock et al., 1999; Ozgul et al., 2014), and also enjoy benefits to dispersal as a result of increases to the size of dispersing units (Young, 2003). Our study shows that dominant females in larger groups also benefit from increased fecundity and body mass, as well as the improved survival and growth of their pups, and that these benefits are higher during harsh conditions. The direct benefits obtained by living in larger groups should encourage subordinates to delay dispersal and provide alloparental care, if the latter improves recruitment and group size (Kingma et al., 2014; Kokko et al., 2001), and should similarly promote the tolerance of offspring beyond nutritional independence by dominants. Selection for delayed dispersal and alloparental care will be further enhanced by indirect benefits resulting from high levels of within-group relatedness (Hamilton, 1963). Additionally, being able to successfully reproduce under recurring environmental harshness could improve dominant female fitness by reducing fitness variance, even at the cost of mean fitness ('bet-hedging': Koenig & Walters, 2015; Rubenstein, 2011; Sæther & Engen, 2015).

Another benefit of living in larger groups that is often overlooked is the ability of such groups to persist through periods of environmental harshness, which can generate substantial indirect fitness benefits (Akçay & Cleve, 2016; Heinemann et al., 1999). Such benefits will be especially high for species with high levels of within-group relatedness, such as meerkats (Dyble & Clutton-Brock, 2020). There is also evidence that larger group size reduces the likelihood of group extinction in the social cichlid *Neolamprologus pulcher* (Heg et al., 2005) and recent work suggests that similar benefits operate in meerkats (C. Duncan, M.B. Manser, & T.H. Clutton-Brock, under review; M. Paniw, C. Duncan, F. Groenewoud, M.B. Manser, A. Ozgul, & T.H. Clutton-Brock, in prep). Important questions concerning the benefits of larger groups and the mechanisms that determine group size remain to be answered. For instance, it is currently unclear whether our results could not be partly explained by positive correlations between group size and range size, or territory quality, particularly during droughts. However, even if this were so, it could still be the case that larger groups are able to defend better territories, rather than better territories leading to larger groups. To address this, researchers should focus on explicitly modelling spatial autocorrelation to account for such confounding effects (Koenig, 1999). In addition to group size effects on fecundity, relationships might also exist between group size, climate and adult survival, as has recently been shown for superb starlings *Lamprotornis superbus* (Guindre-Parker & Rubenstein, 2020). It would be worthwhile to assess whether such survival benefits exist for meerkats, which should further improve our understanding of the role of environmental variation on individual fitness and the evolution and maintenance of cooperative breeding.

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## AUTHORS' CONTRIBUTIONS

F.G. and T.C.-B. conceived of the study; F.G. organised the data and performed all the analyses; F.G. wrote the first draft; all authors contributed critically to the drafts and gave final approval for publication.

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