

**Social conflict and costs of cooperation in meerkats are reflected in measures of stress hormones**

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Short title: Social conflict and stress in meerkats

## **Abstract**

Measures of glucocorticoid stress hormones (e.g. cortisol) have often been used to characterize conflict between subordinates and dominants. In cooperative breeders where subordinates seldom breed in their natal group and assist in offspring rearing, increases in subordinate glucocorticoid levels may be caused by conflict among subordinates as well as by the energetic costs of helping behaviour and fluctuations in food availability may exacerbate these effects. During a 6-year study of Kalahari meerkats (*Suricata suricatta*), we investigated how social, environmental, and individual characteristics influenced subordinate plasma cortisol levels. Subordinate females, who are often the target of aggression from dominant females, had higher cortisol levels when the dominant female in their group was pregnant while the cortisol levels of subordinate males were unaffected by the reproductive state of dominant females. Subordinates of both sexes had higher cortisol levels if they belonged to groups i) where neither of the dominant breeders in the group were their parents, ii) that contained a high proportion of subordinate females, or iii) that were either very large or very small, especially when the weather was cold and dry. Subordinates in groups containing young pups had higher cortisol levels. Finally, cortisol levels were higher in subordinates of both sexes if they were lighter for their age or had lost little body mass the night prior to sampling. Our results show how that both social conflict and cooperative behaviour can elevate glucocorticoid levels in subordinates and that both effects can be modified by variation in climate and food availability.

**Key words:** Animal societies, Cooperative breeding, Glucocorticoids, Meerkats,  
Sociality

## **Introduction**

Group-living is associated both with direct and indirect benefits for group members (Jennions and MacDonald 1994; Dugatkin 1997; Clutton-Brock 2002; Koenig and Dickinson 2004; Clutton-Brock 2009). These benefits are offset by direct competition between group members that generate conflicts of interest and lead to regular aggression involving threats and, less commonly, to fighting and eviction or death (West et al. 2002). Circumstances likely to generate conflict between individuals are commonly associated with increases in physiological indicators of stress (Sapolsky 1982; Creel 2001; Abbott et al. 2003; Creel, 2001; Goymann and Wingfield 2004; Creel et al., 2013a) and a wide range of studies have shown that adverse environmental and social conditions can raise circulating levels of the stress hormones glucocorticoids (cortisol and corticosterone).

Glucocorticoids are released by the hypothalamic-pituitary-adrenal (HPA) axis, which is activated in response to predictable or unpredictable environmental challenges (Sapolsky et al. 2000). Glucocorticoids at baseline levels help to maintain homeostasis and coordinate important daily or seasonal rhythms (Sapolsky et al. 2000; Romero 2002; Landys et al. 2006;). Glucocorticoids released following an environmental challenge can trigger adaptive shifts in behaviour or physiology that assist in the maintenance of homeostasis through these environmental challenges (Sapolsky et al. 2000; McEwen and Wingfield 2003; Romero 2004) and are linked with energy mobilization and may provide a proxy of the energetic expenditure associated with this maintenance of constancy through change (Sapolsky et al. 2000; Romero 2002; McEwen and Wingfield 2003). Increased glucocorticoid levels may

therefore occur where individuals experience either more challenging (Bonier et al. 2009) or more energetically demanding (McEwen and Wingfield 2003; but see Romero et al. 2009) environments.

In social species, glucocorticoid concentrations are affected by intragroup conflict, such as conflict between dominants and subordinates, and may reflect its costs (Creel 2001; Goymann and Wingfield 2004; Creel et al. 2013a). For example, in some group-living birds and mammals where dominance is acquired and maintained through aggressive interactions, subordinates have higher glucocorticoid levels than dominants (Goymann and Wingfield 2004) whereas in other species dominants have higher glucocorticoid levels perhaps because they exhibit a higher frequency of aggressive interactions (Creel, 2005; Creel et al., 1996). In cooperative breeding species, subordinate glucocorticoid levels may also be influenced by other sources of intra-group conflict beyond just that occurs between dominants and subordinates. For example, in species where subordinates queue for the dominant breeding position, subordinate glucocorticoid levels may also be affected by intra-group conflict among subordinates. In such species, when a dominance vacancy arises in the social group, the oldest or heaviest subordinate may have a higher probability of acquiring dominance. Older or heavier subordinates may use aggression or threats to maintain that advantage in age or weight (e.g., by evicting similar-aged individuals: Wong et al. 2008; Thavarajah et al. 2014). Consequently, subordinates in groups with many same-sex subordinates queuing for dominance or those that are younger or lighter than their nearest age-matched same-sex rival could exhibit higher glucocorticoid levels because of the

aggression they receive from other same-sex subordinates. Alternatively, heavier or older subordinates may instead exhibit higher glucocorticoid levels due to the energetic costs associated with aggression directed at individuals lower down in the dominance queue.

Intra-group conflict is unlikely to be the only cause of variation in subordinate glucocorticoid levels in cooperative breeders. Subordinates in cooperatively breeding species exhibit helping behaviours within their social groups such as assisting in rearing of offspring produced by dominant breeders. These helping behaviours typically carry energetic costs (Russell et al. 2002) that may in turn elevate subordinate glucocorticoid levels as glucocorticoids are metabolic hormones associated with energetic expenditure (Sapolsky et al. 2000; Romero 2002; McEwen and Wingfield 2003).

The effects of intra-group conflict and energetic costs of helping on subordinate glucocorticoid levels are likely influenced by either environmental conditions or other features of the social group. For example, subordinates may experience less competition or overt aggression from dominants when food resources are high (Young et al. 2010; Nichols et al. 2012), when group size is small or when subordinates are closely related to the dominants (Young et al. 2006; Clutton-Brock et al. 2010). Increases in subordinate glucocorticoid levels caused by exhibiting cooperative behaviour may also be reduced when subordinates experience high food availability or when they are in large groups because the energetic costs of helping are lowered due to increased food or because the relative

contributions to helping are lowered in large groups (Clutton-Brock et al. 2001, 2002, 2003).

To date, few studies have simultaneously examined how multiple social, environmental, and individual factors affect the glucocorticoid levels of social subordinates (but see Arnold and Dittami, 1997; Goymann et al., 2001; Muller and Wrangham, 2004; Rubenstein 2007; Rubenstein and Shen 2009). Here, we measured plasma glucocorticoids (cortisol) of subordinate meerkats during 6 years of study across a 10-year period (2004-2014). Our objectives were to address how subordinate glucocorticoid levels were affected by 1) conflict between subordinates and dominants, 2) conflict among same-sex subordinates, 3) presence of pups receiving cooperative care from subordinates within the group, and 4) how variation in food availability and characteristics of the social group (group size, group sex ratio, relatedness to the dominant breeders) interact with these other factors to influence subordinate glucocorticoid levels.

Meerkats are obligate cooperative breeders and live in groups of 3-50 individuals. Each group contains a single female and male that are behaviourally dominant to all other subordinates of the same sex in the group (Clutton-Brock et al. 2006; Hodge et al. 2008; Spong et al. 2008). Subordinate females and males remain in the group and contribute to several cooperative behaviours associated with successful rearing of offspring produced by the dominant breeders (Clutton-Brock et al. 1999, 2000, 2004). Dominant females sometimes violently evict subordinate females (Clutton-Brock et al. 1998a; Young et al. 2006) and both subordinate and dominant females will occasionally kill offspring produced by females in the other

social rank (Clutton-Brock et al. 1998b; Young and Clutton-Brock, 2006; Clutton-Brock et al., 2010). Dominant male meerkats monopolize reproduction within the group (Spong et al. 2008) even though subordinates are capable of reproducing (O’Riain et al. 2000). Subordinate males are submissive towards dominant males (Kutsukake and Clutton-Brock 2008) but they are not evicted from their natal group (Clutton-Brock et al. 1998b).

Dominant female meerkats are more aggressive towards subordinate females when they are pregnant (Kutsukake and Clutton-Brock 2006; Young et al. 2006; see also Creel et al., 1992 for a similar result in another social mongoose species) and both dominant females and males are more aggressive to same-sex subordinates in larger groups (Kutsukake and Clutton-Brock 2006; Clutton-Brock et al. 2008, 2010). We therefore predicted that glucocorticoid levels would be higher in subordinate females when the dominant female was pregnant and in subordinates of both sexes in larger groups. Because dominant females tend to target their closest reproductive competitors (i.e., the heaviest or oldest subordinate females in the group: Clutton-Brock et al. 2008, Kutsukake and Clutton-Brock, 2008; Clutton-Brock et al. 2010 Young et al. 2006), we predicted that subordinate females that were older and heavier would have the highest glucocorticoid levels when the dominant female was pregnant.

Subordinate male meerkats voluntarily disperse and breed outside of their natal group (Clutton-Brock et al. 1998b; Young et al. 2005, 2007). In order for females to reproduce, they must either acquire dominance in their natal group or disperse and found their own group, the latter of which is unlikely due to the low



probability of surviving dispersal (Stephens et al. 2005). When a dominance vacancy arises in the social group, the oldest (both females and males: Hodge et al. 2008; Spong et al. 2008) and heaviest (only females: Hodge et al. 2008; Spong et al. 2008) subordinate has a higher probability of acquiring dominance. Older or heavier subordinates may use aggression or threats to maintain that advantage in age or body mass (e.g., by evicting similar-aged individuals: Young et al. 2006; Thavarajah et al., 2014). We therefore predicted that the greater the skew towards female competitors in the social group, the higher cortisol levels would be in female, but not in male subordinates. We also predicted that subordinates that were lighter than same-sex intra-group competitors would have higher cortisol levels perhaps reflecting the greater aggression they receive from older or heavier same-sex subordinates in their group.

Subordinate females and males care for dependent pups soon after they are born (“babysitting”: Clutton-Brock et al. 1998a, 2000) and provision them with food items (“pupfeeding”, Clutton-Brock et al., 1998a, 2000; Brotherton et al. 2001; Clutton-Brock et al. 2004). The presence of dependent pups in the group (either during babysitting or pupfeeding) may carry substantial energetic costs associated with pup rearing (Clutton-Brock et al., 1998a, 2000; Scantlebury et al. 2002; Russell et al. 2003; Scantlebury et al. 2004). Because energetic expenditure may be positively associated with glucocorticoids (Sapolsky et al. 2000; Romero 2002; McEwen and Wingfield 2003), subordinate glucocorticoid levels should therefore be elevated when there are dependent offspring in the social group. However, these energetic costs may be ameliorated when food availability is high or when there are

many subordinates in the group to share the workload. Meerkats experience dramatic seasonal changes in rainfall and temperature from a cold and dry winter (~May-September) to a hot and wet summer (~October-April). Meerkats experience a more favourable growing environment during the summer months when it is hot and wet (English et al. 2011, 2014), indicative of increased food availability (Doolan and Macdonald 1996). We therefore predicted that the effects of cooperative pup rearing on the glucocorticoid levels of subordinates would be influenced by recent weather conditions and subordinate foraging success. Finally, we predicted that elevations in subordinate glucocorticoid levels when pups were present in the group would be less apparent in large groups where the workload of caring for pups is reduced.

## **Materials and Methods**

### *Study Area and Species*

We studied individually-marked meerkats in 20 different social groups at the Kuruman River Reserve (26° 58' S, 21° 49' E; ~63 km<sup>2</sup> in size) in the Northern Cape, South Africa using protocols that were approved by the Animal Ethics Committee at the University of Pretoria (#EC011-10, Pretoria, South Africa) and the Northern Cape Conservation Authority. All protocols adhered to ABS/ASAB guidelines for the ethical treatment of animals. Individuals were uniquely and permanently marked at emergence from their natal den (around 20-30 days after birth) with microchip transponders (Identipet®, Johannesburg, South Africa). Small unique dye marks

were also applied when pups first emerged and reapplied throughout their life so that they could be identified visually.

Meerkats live in social groups composed of mostly close relatives with subordinates often being closely related to the dominant breeding pair (Nielsen et al. 2012). The dominant breeding pair produces ~90% of the offspring (Hodge et al. 2008; Spong et al. 2008) and subordinate females and males contribute to the rearing of the offspring (Clutton-Brock et al., 1998a; Doolan & Macdonald 1999; Clutton-Brock et al. 2001, 2002). Both subordinate females and males are physiologically capable of reproducing around one year of age and sometimes produce offspring within their natal group (O’Riain et al. 2000; Young et al. 2007; Spong et al. 2008). Males but not females frequently engage in extra-group roving (Young et al. 2007; Mares et al. 2014) where they can sire offspring with unrelated females outside of their groups (Young et al. 2005, 2007; Spong et al. 2008).

Meerkats first emerge from their natal burrow when they are around 20-30 days of age. During their first month of life, pups stay at the natal burrow with an older subordinate (‘babysitter’: Clutton-Brock et al. 1998a) while the rest of their social group goes foraging away from the sleeping burrow for the entire day. From 1 to 3 months of age while the pups are foraging with the group, they are provisioned with food items that were found by older subordinates in their social group (Brotherton et al. 2001). After around 3 months, meerkats obtain the majority of their food by foraging independently (Thornton 2008).

#### *Capture Protocol*

We measured the plasma cortisol levels of subordinate meerkats that were older than >90 days of age (i.e., independent foragers: Thornton 2008), socially subordinate, and not known to be pregnant (assessed visually and via patterns of weight gain). Each meerkat was captured approximately every 3-6 months during its lifetime in our study population. Meerkats are habituated to the presence of humans and this allowed us to capture them by hand. We assume that all individuals and groups were equally habituated to humans and these blood sampling procedures, though it is unlikely that differences in habituation would produce systematic biases in our data. Meerkats were gently picked up by their tail, placed into a clean pillowcase, and anaesthetized using 4% isoflurane (Isofor, Safe Line Pharmaceuticals, Johannesburg, South Africa) mixed with oxygen administered via a gas mask attached to a portable vaporizer. After full sedation, isoflurane dosage was lowered to 1-2% and a blood sample was obtained from the jugular vein using a 25G needle and 2 ml syringe. Blood samples were placed in a cooler with wet ice immediately after collection in the field for up to 1 hour before being centrifuged (500 g for 10 min) whereupon the plasma was drawn off and stored at -20 C until analysis. We limited the effect of any circadian patterns in plasma cortisol secretion on our results by only analysing samples that were collected in the morning or mid-morning (0610-1208 h) immediately after meerkats emerged from their sleeping burrow (which varies seasonally: Thornton et al., 2010) or soon after they had started foraging. Most of these samples (n = 322/387 samples) were collected from 0610-0900 h immediately after they emerged from the sleeping burrow with others (n = 65) being collected soon after they had started foraging (from 0901-1208 h). If

we included time of day at which we obtained the sample into our main model (Table S2), the effect of sampling time was not statistically significant ( $t=-0.29$ ,  $P=0.77$ ) and our main results did not change (results not shown).

#### *Effect of capture on plasma cortisol levels*

Capture and handling substantially elevates plasma glucocorticoid levels in mammals (Fletcher and Boonstra 2006; Delehanty and Boonstra 2009) with baseline glucocorticoid levels thought to be reflected in blood samples collected within 3 min of initial capture (Romero and Reed 2005; Delehanty and Boonstra 2009). We recorded the total amount of time taken from initial capture by hand until the blood sample was acquired at each capture and we used this to assess how capture stress influences plasma cortisol levels (Fig. S1). All together, we measured cortisol levels in a total of 387 plasma samples (154 from females, 233 from males) collected 2-18 min (median = 5 min, interquartile range = 4-7 min) after capture from 179 subordinate meerkats.

Using all these samples, we developed a profile of how capture stress affected plasma cortisol levels (Fig. S1). Cortisol levels significantly increased as the amount of time from initial capture to blood sample acquisition increased (Table S1, Fig. S1). The significant non-linear effect of sampling time (Table S1) and visual inspection of the data (Fig. S1) suggests that cortisol levels peaked about 10 min after initial capture and then declined. Cortisol levels had a low repeatability ( $R=0.04$ ; Lessels and Boag 1987) in a linear mixed-effects model containing only the intercept and a random intercept term for individual identity, capture group identity, and year. In addition, the inclusion of individual identity in this model did

not improve fit compared to the same model lacking the random intercept term for individual identity ( $\chi^2 = 0.39$ ,  $df = 1$ ,  $P=0.53$ ).

### *Measuring body mass and foraging success*

Habituated meerkats were trained to go onto a portable balance (weighed to the nearest g) for a small food (crumb of hard-boiled egg) or water reward. During each visit to the group (3-5 times per week), we weighed each meerkat present in the morning immediately after emergence from their sleeping burrow but before foraging had commenced and then again in the evening after foraging for that day was completed immediately before the meerkats entered their sleeping burrow. Using these measurements of mass, we obtained estimates of age-corrected body mass, mass-corrected foraging success, and the mass of the same-sex similar-aged individuals. Because the birth date of each meerkat was known, we calculated age-corrected body mass as a measure of body condition. We controlled for any short-term fluctuations in body mass by averaging the morning body mass of individuals over the 30 days prior to capture and then using the residuals from a general linear model (response variable was average morning body mass, predictor variable was age) to estimate age-corrected body mass. We estimated daily foraging success as the evening body mass minus the morning body mass within the same day and took the average daily foraging success over the previous 30 days prior to capture. Because larger meerkats may have higher absolute daily foraging success, we estimated mass-corrected foraging success as the residuals from a general linear model (response variable was daily foraging success, predictor variable was morning body mass).

### *Documenting environmental characteristics*

Rainfall was measured each day using a standard rain-gauge located at our study site. Daily temperature was recorded every hour each day using an alcohol thermometer that was suspended in the shade. This allowed us to calculate the average daily temperature as well as the lowest temperature that had occurred on that day. To obtain estimates of environmental conditions prior to capture, we summed rainfall, obtained the lowest temperature experienced for the 30 days prior to capture, and took the average daily temperature for the previous 30 days prior to capture. Meerkats that we captured in the summer ( $n = 251$ ) experienced more rain (mean  $\pm$  SE:  $19 \pm 1.6$  mm cumulative rainfall), a higher daily average temperature ( $23 \pm 0.28$  C), and less extreme low temperatures (average minimum temperature:  $5.6 \pm 0.44$  C) for the month prior to capture than those that we captured in the winter ( $n = 136$ ; rainfall:  $9.4 \pm 0.8$  mm; average daily temperature:  $12.7 \pm 0.22$  C; average minimum temperature observed:  $-5.24 \pm 0.25$  C). We used a principal component (PC) analysis (using a correlation matrix in package *ade4* in R version 3.02; R Development Core Team 2009) to develop a single measure of environmental conditions that reflects both precipitation and temperature for the 30 days prior to capture. PC1 explained 74.5% of the variation in rainfall and temperature. The loadings for PC1 for cumulative rainfall (0.46), average daily temperature (0.61), and the lowest temperature recorded (0.64) indicated that high scores of PC1 corresponded to hot and wet conditions whereas low scores corresponded to cold and dry conditions.

### *Documenting group-level characteristics*

We visited meerkat groups for approximately 3-5 hours in the morning and for approximately 1-3 hours in the evening about once every two to three days throughout each year of study. During each visit, we recorded the number and individual identity of males and females that were present in the group to obtain the identity of the dominant female and male, measures of group size, sex ratio of the group, and the presence, age, and mass of same-sex competitors. Pregnancy status of the dominant female was determined by noting steady mass gain and visible swelling of the abdomen and nipples. The end date of a pregnancy of a dominant female was noted by changes in the physical appearance of dominant females, dramatic overnight mass loss, and the presence of subordinate individuals 'babysitting' (Clutton-Brock et al. 1998a) at the sleeping burrow while the rest of the group went foraging. Presence of pups <90 days of age was determined either by direct observation or indirectly by the presence of babysitters at the sleeping burrow. Group size and group sex ratio were averaged for the month prior to capture and blood sampling to control for short-term fluctuations in group size or group sex ratio.

#### *Plasma cortisol assay*

We measured total plasma cortisol levels (cortisol bound and unbound to corticosteroid-binding globulin) using an assay that has been previously validated for use in meerkats (Coat-a-Count, Siemens Diagnostic Products Corporation, Los Angeles, USA; Carlson et al. 2004, Carlson et al. 2006a, 2006b). A series of known calibrators of cortisol were assayed to set up the standard curve. Plasma samples (25 $\mu$ l) and <sup>125</sup>I-labelled cortisol (1000 $\mu$ l) were added to assay tubes in duplicate



and briefly vortexed. Assay tubes were incubated in a water bath at 37°C for 45 mins. Bound and free <sup>125</sup>I-labelled cortisol was separated by decanting the excess label from the assay tubes, which were then counted in a Cobra gamma counter for 1 min. A calibration curve was then used to convert counts into cortisol concentration using the spline curve function. A serial dilution of a plasma sample containing a high concentration of cortisol paralleled the standard curve (ANCOVA,  $P > 0.05$ ). The antibody is highly specific for cortisol with cross reactivity to other hormones being 76% with prednisolone, 11.4% with 11-deoxycortisol, 2.3% with prednisone and <1% with aldosterone, corticosterone, cortisone, estriol, estrone and pregnenolone. Intra-assay coefficient of was 5.2%. Inter-assay coefficient of variation for a low control was 5.7%,  $38.7 \pm 1.3$  ng/ml ( $n = 9$  assays) and for a high control 9.1%,  $216 \pm 19.9$  ng/ml ( $n = 9$  assays). The sensitivity of the assay was 1.9 ng/ml.

### *Statistical Methods*

We developed a linear mixed-effects model (using lme4 version 1.1-12: Bates et al. 2015) in R (version 3.31, R Development Core) that incorporated different environmental, social, and individual characteristics as well as interactions with sex or interactions among these different variables to test our predictions (see *a priori* predictions indicated in the Introduction for why we included each term and interactions with other terms). Variables included were a combination of individual (age, sex, age-corrected body mass, mass-corrected foraging success), environmental (PC1 that reflects cumulative rainfall, average daily and minimum temperatures for previous month: see above), and social (dominant female

pregnancy status, group size, group size<sup>2</sup>, proportion of females in the group, presence of pups <90 d of age in the group, difference in body mass of the nearest same-sex and similar-aged individual) characteristics of their environment immediately prior to capture. We also included specific interactions in these models such as examining how the effects of body mass, foraging success, or weather patterns might ameliorate or magnify the effects of characteristics of the social group on cortisol levels. We included a covariate for the time it took to obtain the blood sample from initial capture (stress response shown in Fig. S1).

We conducted a separate analysis on a subset of our dataset for which we had measures of body mass from subordinates the night prior to their capture and blood sampling and the morning of their capture and blood sampling (n=142 samples from 96 individuals). This allowed us to estimate the association between overnight mass loss prior to capture and blood sampling and plasma cortisol levels. In this model, we only included variables that were significant predictors of subordinate cortisol levels in our larger analysis described above (see Table S1 for list of variables included). We calculated overnight mass evening mass minus the morning mass and then estimated the proportion of body mass lost overnight by dividing overnight mass loss by evening mass the night prior to capture.

In these models, we included non-linear terms of group size and capture to bleed time because of the possibility of non-linear effects on cortisol levels. We included interactions between the non-linear term for group size (group size<sup>2</sup>) and whether there were pups in the group, recent weather conditions, and recent foraging success. Because we had repeated samples on the same individuals

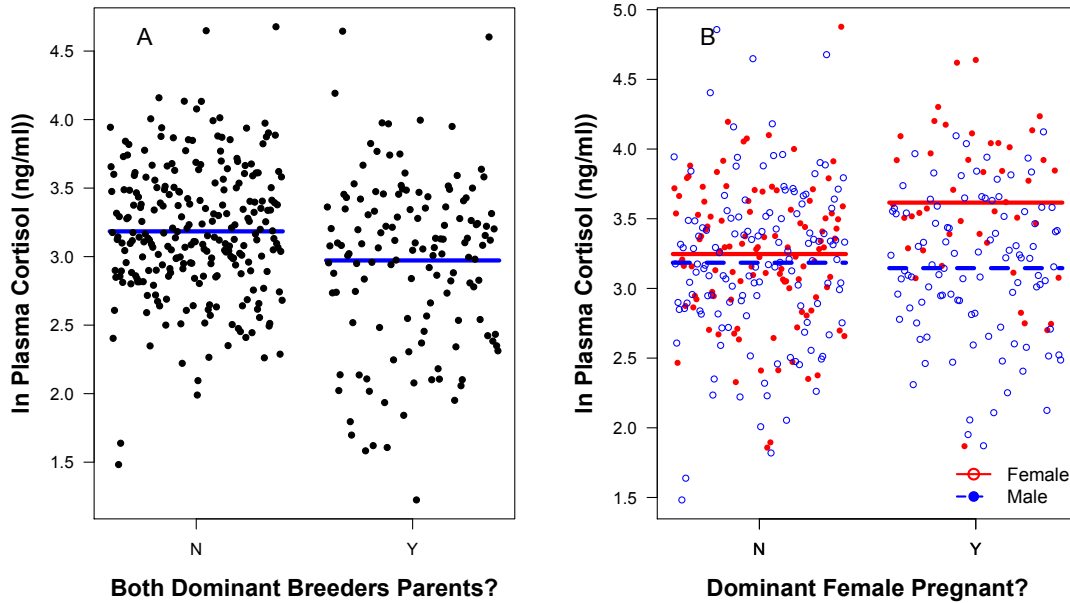
(n=179), in the same social groups (n=20), and in the same years (n=6), we included a random intercept terms for individual identity, social group, and year. We used a graphical approach to confirm the normality and homoscedasticity of the residuals from the models. We ln transformed cortisol levels and age to improve normality and homoscedasticity of the residuals and present ln transformed plasma cortisol levels (ng/ml) in the figures but present untransformed data within the text. All continuous variables in the models were standardized (mean of 0, variance of 1), which allows the magnitude of the effect sizes among the different variables to be compared (Schielzeth 2010). We estimated the conditional  $R^2$  using the approach outlined by Nakagawa and Schielzeth (2010) using the package MuMin (version 1.15.6, Barton 2014). Denominator degrees of freedom and P-values were estimated using Satterthwaite approximation using lmerTest (version 2.0-32, Kuznetsova et al. 2015). Unless otherwise indicated, below we present mean  $\pm$  SE.

## Results

### *Effects of conflict between subordinates and dominants*

Subordinates in groups where both of the dominant breeders were their parents (n=135) had significantly lower cortisol levels than those in groups where both dominant breeders were not their parents (n=252,  $F_{1,99} = 5.91$ ,  $P=0.017$ , Table S1, Fig. 1A) and there was no evidence that this effect was sex-specific (females  $b = -0.26 \pm 0.14$ ; males:  $b = -0.21 \pm 0.12$ ; sex x relatedness interaction,  $F_{1,213} = 0.07$ ,  $P=0.79$ , Table S2).

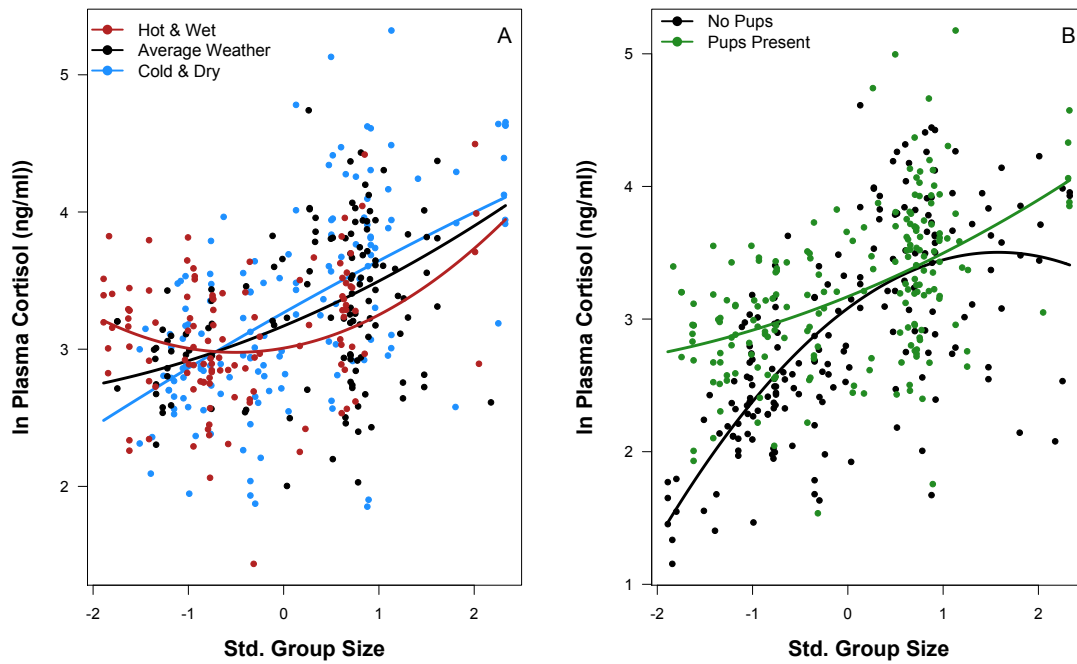
**Figure 1.** A) Subordinate female and male meerkats that lived in a group where both dominant breeders were their parents had significant lower plasma cortisol levels than those that lived in group where the dominant breeders were not their parents (Table S1). B) Subordinate females but not males that lived in groups where the dominant female was pregnant had higher plasma cortisol levels (Table S1). Partial plots (from model in Table S1) are shown that took the median values for other covariates in the model. Plasma cortisol levels were ln transformed.



There was a significant interaction between sex and the pregnancy status of the dominant female on subordinate cortisol levels ( $F_{1,339} = 5.34$ ,  $P=0.021$ , Table S1, Fig. 1B). Subordinate females in groups where the dominant female was pregnant ( $n=45$ ) had significantly higher plasma cortisol levels than those in groups where the dominant female was not pregnant ( $n=109$ ,  $b= 0.35 \pm 0.13$ ,  $t_{332}=2.67$ ,  $P=0.008$ , Table S2). Subordinate males in groups with pregnant dominant females ( $n=100$ ) had similar cortisol levels as those in groups without a pregnant dominant female ( $n=133$ ,  $b= -0.015 \pm 0.09$ ,  $t_{318}=-0.16$ ,  $P=0.87$ , Table S2). There was no evidence that heavier or older subordinate females in the group had higher cortisol levels than lighter or younger subordinates when the dominant female was pregnant as indicated by the lack of 3-way interactions between sex, pregnancy status of the dominant female, and either subordinate age ( $F_{1,335} = 0.38$ ,  $P=0.54$ , Table S1) or age-corrected body mass ( $F_{1,342} = 0.57$ ,  $P=0.45$ , Table S1). Subordinates that received more dominance assertions from the dominant female did not have higher cortisol levels ( $F_{1,338} = 2.7$ ,  $P=0.1$ , Table S1).

Average group size varied among groups across the 6 years of study ( $15.3 \pm 0.31$  individuals, range = 3.8-29.5). Subordinates in larger groups had higher cortisol levels (Fig. 2) but the effects of group size on subordinate cortisol levels were influenced by recent weather conditions (Fig. 2A). Specifically, subordinate cortisol levels increased as group size increased but the rate of increase was higher when weather conditions had been cold and dry for the month prior to capture compared to when it had been hot and wet for the month prior to capture (interaction between weather and group size,  $b = -0.1 \pm 0.05$ ,  $t_{202} = 2.12$ ,  $P=0.035$ , Table S2, Fig.

**Figure 2.** The effects of group size on subordinate meerkat cortisol levels were influenced by recent weather conditions and whether or not there were pups <90 d of age in the group. A) Subordinates in moderate to large groups tended to have lower cortisol levels if the weather had recently been hot and wet. B) Subordinates in groups containing pups had higher cortisol levels especially if they were in very small or very large groups. In groups lacking pups, subordinate cortisol levels peaked at intermediately sized groups. Partial plots (from model in Table S1) are shown that took the median values for other covariates in the model. Weather conditions were a continuous variable in our statistical analyses (Table S1) but here are shown with very cold and dry weather conditions, average (median), or very hot and wet conditions. Group size was standardized (mean of 0, variance of 1). Plasma cortisol levels were ln transformed.



2A). This meant that in moderate or large groups, subordinates had higher cortisol levels when the weather had been cold and dry compared to if it had been hot and wet (Fig. 2A). However, in very small groups, subordinates tended to have higher cortisol levels if it had been hot and wet compared to when it had been cold and dry (Fig. 2A).

#### *Effects of conflict among subordinates*

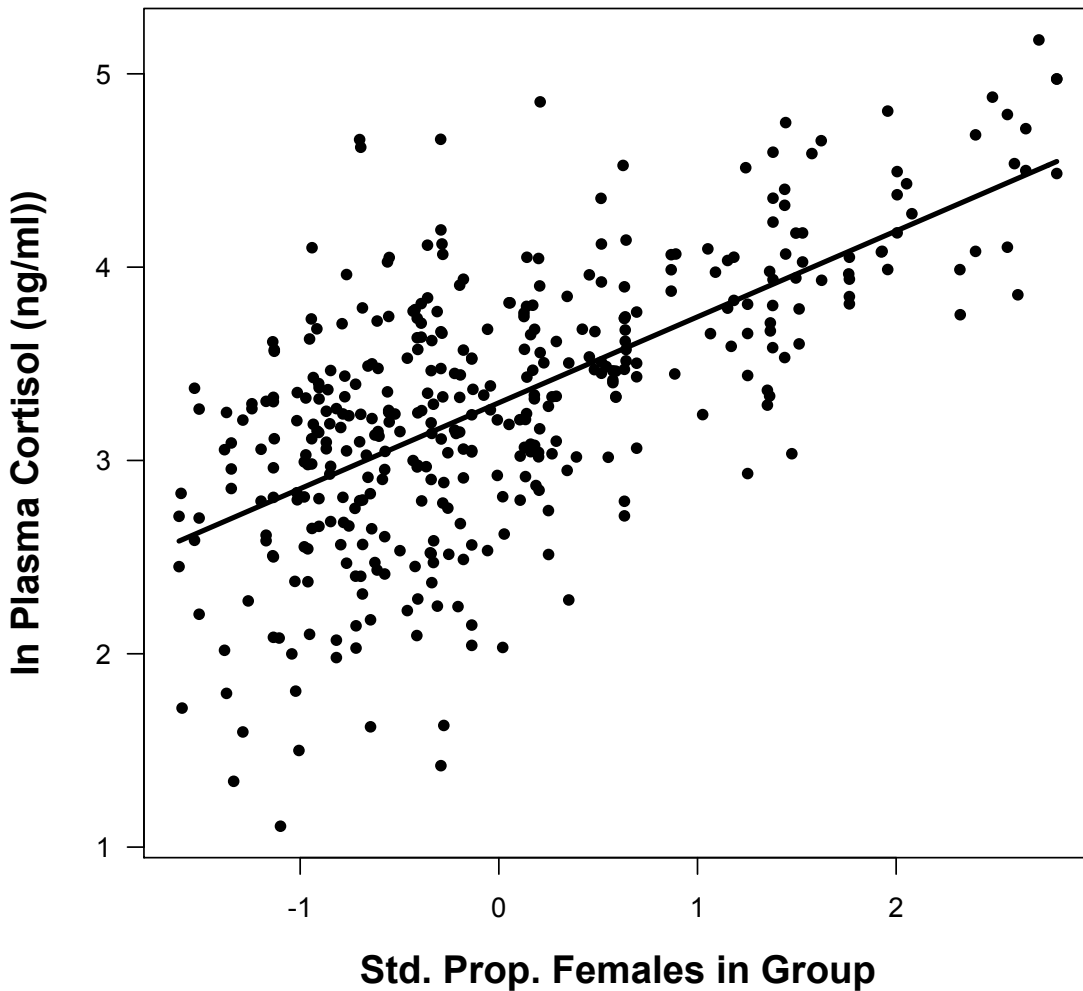
The proportion of females in a social group varied across the 6 years of our study ranging from groups consisting of 19 to 73% subordinate females (mean = 0.39). Subordinate females ( $b = 0.26 \pm 0.12$ ) and males ( $b = 0.44 \pm 0.11$ ) living in groups containing more subordinate females relative to group size had significantly higher plasma cortisol levels ( $F_{1,168} = 16.88$ ,  $P < 0.0001$ , Table S1, Fig. 3) and this effect was not sex-specific ( $F_{1,301} = 1.43$ ,  $P = 0.23$ , Table S2).

Subordinates were relatively close in body mass to their same-sex competitor that they were closest to in age ( $-23.6 \pm 4.6$  g, range =  $-370.2$ - $231.5$  g). Subordinates that were heavier than their nearest rival in the group did not have higher plasma cortisol levels ( $F_{1,280} = 1.01$ ,  $P = 0.31$ , Table S1) regardless of their sex ( $F_{1,275} = 1.72$ ,  $P = 0.19$ , Table S1).

#### *Effects of presence of dependent pups in the social group*

The presence of pups in the group influenced subordinate cortisol levels but these effects depended upon the number of subordinates in the group (pup presence  $\times$  group size<sup>2</sup>,  $F_{1,324} = 14.5$ ,  $P = 0.0001$ , Table S1). Subordinates in very small or very large groups had higher cortisol levels if there were pups ( $< 90$  d) present in the group ( $n = 195$ , Table S1, Fig. 2B). In groups without pups ( $n = 192$ ), subordinate

**Figure 3.** Subordinate females and males in groups where a higher proportion of group members were females had significantly higher plasma cortisol levels. Partial plots (from model in Table S1) are shown that took the median values for other covariates in the model. Proportion of females in the group was standardized (mean of 0, variance of 1). Plasma cortisol levels were ln transformed.



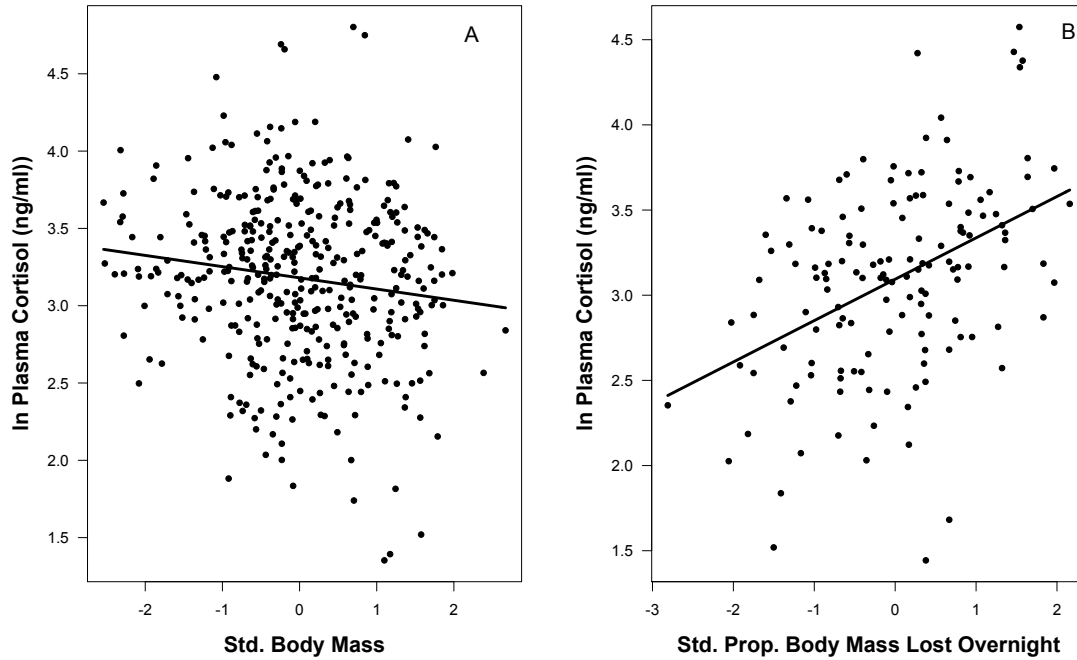


cortisol levels increased significantly as group size increased (females:  $b = 0.37 \pm 0.18$ ,  $t_{212} = 2.09$ ,  $P=0.039$ ; males:  $b = 0.52 \pm 0.14$ ;  $t_{214} = 3.91$ ,  $P=0.0001$ , Table S2, Fig. 2B) and there was also evidence of a significant non-linear association where subordinate cortisol levels peaked in medium sized groups (females:  $b = -0.32 \pm 0.09$ ,  $t_{301} = -3.4$ ,  $P=0.0007$ ; males:  $b = -0.16 \pm 0.06$ ;  $t_{215} = -2.49$ ,  $P=0.014$ , Table S2, Fig. 2B). In groups with pups, subordinate cortisol levels also increased with group size (females:  $b = 0.34 \pm 0.14$ ,  $t_{156} = 2.46$ ,  $P=0.015$ ; males:  $b = 0.27 \pm 0.14$ ;  $t_{139} = 1.93$ ,  $P=0.056$ , Table S2) but there was no evidence that subordinate cortisol levels peaked at an intermediate group size in such groups (effect of group size<sup>2</sup> in groups with pups, females:  $b = 0.02 \pm 0.07$ ,  $t_{229} = 0.29$ ,  $P=0.77$ ; males:  $b = 0.05 \pm 0.08$ ;  $t_{246} = 0.61$ ,  $P=0.54$ , Table S2). The lack of non-linear relationship between group size and subordinate cortisol levels in groups with pups meant that subordinates in the smallest or largest groups had much higher cortisol levels compared to those in similar sized groups lacking pups. There was no evidence that the effects of pup presence and group size on subordinate cortisol levels differed between the sexes (Table S1). The effects of the presence of pups in the group on subordinate cortisol levels were not influenced by recent weather conditions experienced by subordinates of either sex (Table S1) or their recent foraging success (Table S1).

#### *Effects of weather and individual-state*

The effects of recent weather conditions on subordinate cortisol levels depending upon group size (see above). Plasma cortisol levels did not differ between subordinate females ( $n=154$ ,  $29.3 \pm 1.69$  ng/ml, range = 2.9-176.06 ng/ml) and males ( $n=233$ ,  $27.31 \pm 1.45$  ng/ml, range = 2.54-140.12 ng/ml,  $F_{1,196} = 1.16$ ,

**Figure 4.** Subordinate female and male meerkats that A) had a higher body mass for their age had significantly higher plasma cortisol levels (Table S1) whereas B) those that had lost a higher proportion of their body mass the night prior to capture had higher plasma cortisol levels (Table S2). Body mass and overnight mass loss were standardized (mean of 0, variance of 1). Partial regression plots (from model in Tables S1 or S2) are shown that took the median values for other covariates in the model. Plasma cortisol levels were ln transformed.



$P=0.28$ , Table S1). Both female and male subordinates that were heavier for their age had slightly but significantly lower plasma cortisol levels (females:  $b= -0.14 \pm 0.08$ ; males:  $b= -0.07 \pm 0.1$ ;  $F_{1,280} = 6.44$ ,  $P=0.012$ , Table S1, Fig. 4A) however, their age at sampling ( $F_{1,215} = 0.3$ ,  $P=0.58$ , Table S1) did not affect their cortisol levels. There was no evidence that the effects of body mass or age on cortisol levels differed between the sexes as indicated by the lack of significant interactions between each of these variables and sex (Table S1). The effects of foraging success on subordinate cortisol levels slightly differed between the sexes ( $F_{1,321} = 3.31$ ,  $P=0.07$ , Table S1) where females ( $b= 0.23 \pm 0.12$ ) but not males ( $b= -0.03 \pm 0.12$ ) with higher foraging success had higher cortisol levels. Subordinates lost between 10.2 % and 0.5% of their body mass overnight (mean  $\pm$  SD,  $4.7 \pm 0.16\%$ ). Subordinates that had lost a lower proportion of their body mass the previous evening had significantly higher plasma cortisol levels ( $b=0.24 \pm 0.06$ ,  $F_{1,110} = 16.99$ ,  $P=0.0001$ , Table S1, Fig. 4B).

## Discussion

Our results are consistent with the hypothesis that subordinate cortisol levels reflect the degree of intra-group conflict between both dominants and subordinates and also among subordinates within the social group. Previous studies in meerkats indicate that dominant females are more aggressive towards subordinate females when they are pregnant (Clutton-Brock et al. 2004; Young et al. 2006) or less related to them (Clutton-Brock et al. 2010). Our results highlight this conflict is reflected in subordinate cortisol levels; subordinate females but not males

had higher cortisol levels when the dominant female was pregnant and subordinates of both sexes had higher cortisol levels when they were in groups where they were unrelated to dominant breeders. Finally, we also found a positive but non-significant association between subordinate cortisol levels and the frequency with which they received dominance assertions from the dominant female. Our results are similar to previous studies in other social mammals showing that subordinate glucocorticoid levels influenced by the amount of aggression they receive from dominants (Goymann et al., Creel, 2005) but that the amount of aggression subordinates receive and associated increases in glucocorticoid levels may be reduced if they are closely related to the dominants (Hackländer et al., 2003). Overall, these results indicate that when dominants direct more aggression at subordinates, it causes a prolonged elevation in subordinate glucocorticoid levels. Thus, subordinate cortisol levels appear to closely reflect the amount of conflict occurring between subordinate and dominant meerkats as has been shown in other social carnivores (Creel 2005).

Subordinates had higher cortisol levels when they lived in larger groups (see also Raouf et al. 2006; Creel et al. 2013b), though the effects of group size on subordinate cortisol levels were moderated by weather and whether there were dependent pups in the group (discussed below). The increase in subordinate cortisol levels in larger groups that we observed may reflect increased conflict between subordinates and dominants as dominant meerkats are more aggressive to same-sex subordinates when in larger groups (Young et al. 2006; Clutton-Brock et al. 2008; Kutsukake and Clutton-Brock 2008; Clutton-Brock et al. 2010). Alternatively,

it may reflect conflict among subordinates for their placement in a dominance queue. In larger groups, subordinate meerkats may have more individuals ahead of them in the dominance queue and experience more aggression from older or heavier same-sex subordinates. There is some evidence of increased aggression among subordinates in larger groups in other group-living species (Caraco 1979) and this may be reflected in higher cortisol levels (Ostner et al. 2008). However, we are unable to distinguish whether subordinates in larger groups have higher cortisol levels due to conflict with dominants or other subordinates.

There was some evidence that the positive effect of group size on subordinate cortisol levels was reduced under favourable weather conditions. Subordinates in large groups that had recently experienced hot and wet weather had lower cortisol levels than those that had recently experienced cold and dry weather. This suggests that the amount of conflict between subordinates and dominants or among subordinates is lower when environmental conditions are favourable. For example, cold temperatures or low food-availability may lower the overall body condition of meerkats (Russell et al. 2002; English et al. 2011, 2014), which could increase the amount of intra-group conflict (Hodge 2009; Young et al. 2010; Nichols et al. 2012). However, we found no evidence that the effects of group size on subordinate cortisol levels were ameliorated when subordinates had recently had high foraging success. Thus, while our results suggest that favourable weather conditions can reduce the cortisol levels of subordinates in large groups, subordinates in large groups that were experiencing high food availability did not have lower cortisol levels.

There was little evidence that the placement of subordinates in the dominance queue affected their glucocorticoid levels. Subordinates that were substantially lighter than their nearest same-sex rival within the group (and therefore lower in the dominance queue) did not have higher cortisol levels. Both subordinate females and males in groups composed of a higher proportion of subordinate females had higher cortisol levels. We had predicted that only subordinate females would have higher cortisol levels if they were in groups with more same-sex competitors because subordinate males can voluntarily come and go from their social group to seek extra-group reproductive opportunities (Young et al. 2007; Mares et al. 2014). The lack of sex differences here is surprising but one explanation is that there is a greater amount of overall intra-group conflict or instability in groups with more subordinate females, which may in turn elevate cortisol levels in both subordinate females and males. Subordinate females but not males are violently evicted from the social group by the dominant female (Clutton-Brock et al. 1998b; Young et al. 2006). In meerkat groups with more females, there may be increased instability in group size or member composition due to an increased frequency of temporary eviction of subordinate females from the group. In group-living animals, increased social instability within the group can elevate glucocorticoid levels in both dominants and subordinates (Sapolsky et al. 1992; Van Meter et al. 2009; but see Gesquire et al. 2011). Although subordinate male meerkats are not known to directly experience conflict between dominant and subordinate females, this increased instability may in turn elevate their own glucocorticoid levels.

Subordinate female and male meerkats had elevated cortisol levels when there were dependent pups present in the group (see also Carlson et al. 2006a, 2006b), though the impact of the presence of pups on subordinate cortisol levels was most evident in very small or very large groups. Cooperative care of offspring can impose substantial energetic costs on subordinates measured both in terms of weight loss (Scantlebury et al. 2002; Russell et al. 2003) and increased energetic expenditure (Scantlebury et al. 2004) during pup rearing. Glucocorticoids are intimately involved in energy balance (Sapolsky et al. 2000) and so it is not surprising that subordinate cortisol levels were elevated during these periods of increased energetic expenditure. We did not find that subordinates in groups with pups that experienced high foraging success or benign weather conditions (hot and wet) had lower cortisol levels, though those in small groups with pups did have higher cortisol levels. Overall, this suggests that the energetic costs of pup rearing for subordinates can be mitigated to some degree if subordinates are in large groups because the workload for each subordinate may be reduced in large groups (Clutton-Brock et al. 2001, 2002, 2003).

Subordinates that were heavier for their age had lower cortisol levels yet we did not find that subordinates with increased foraging success had lower cortisol levels (see also Arnold and Dittami, 1997). Instead, females but not males with elevated foraging success tended to have higher cortisol levels. One possibility to explain these results is that elevated cortisol levels promote foraging behaviour in subordinates (Dallman et al. 2004; Maniam and Morris 2012) thereby generating a positive association between subordinate cortisol levels and their foraging success.

Subordinates with the highest foraging success would also tend to be those that are heavier for their age thereby generating the negative association between body mass and cortisol levels (see also Arnold and Dittami, 1997). However, it is not clear why the association between cortisol levels and foraging success would differ between the sexes so an alternative view is that the positive association between foraging success and cortisol levels in subordinate females is due to increased aggression received from the dominant female. Testing these two alternatives will require experimental increases of either subordinate cortisol levels (to identify if it increases foraging success) or subordinate foraging success (to identify if dominants target subordinates with increased foraging success).

Our results provide a test of some of the predictions regarding the glucocorticoid levels of subordinates due to intra-group conflict (Rubenstein and Shen 2009). First, in support of this model (Rubenstein and Shen 2009), we found that subordinates had lower cortisol levels if they were in groups where the dominant breeders are close relatives (see also Arnold and Dittami, 1997). Our results and those from previous studies in meerkats (Young et al. 2006; Clutton-Brock et al. 2010) and other species (Hackländer et al. 2003) indicating that subordinates receive less aggression from dominants if they are closely related suggesting that the amount of intra-group conflict between dominants and subordinates is reduced in groups where dominants and subordinates are closely related (see also Shen et al. 2014). Second, our results provide mixed support for the prediction that the glucocorticoid levels of subordinates are unaffected by the nutritional state of the dominant breeders. We did not directly measure the



nutritional state of dominant breeders in the group and so we assume that the nutritional state of dominants was increased when it had been hot and wet (when there is more food available: Doolan and Macdonald 1996; English et al. 2011, 2014;) or when the foraging success of subordinates was elevated. Subordinates had higher cortisol levels in larger groups (which may be due to increased conflict between subordinates and dominants or among subordinates: see above), however, this effect was mitigated to some degree if it had recently been hot and wet but not when subordinates had higher foraging success. This suggests that when the nutritional state of dominant breeders increases, subordinate glucocorticoid levels may either be unaffected or slightly decline. Finally, in contrast to this model, we did not find that subordinates in larger groups had lower cortisol levels. Instead, subordinates had higher cortisol levels in larger groups and in groups with a higher proportion of females. Our results are instead consistent with the predictions from a separate model (Shen et al. 2014) showing that intra-group conflict increases with group size in species where sociality had evolved due to the direct benefits to group members associated with living in a group (e.g., lower risk of predation). In meerkats, sociality may have direct benefits to group members such as a lowered risk of predation with increases in group size (Clutton-Brock et al. 1999). Our results therefore provide some support for the prediction by Shen et al. (2014) that intra-group conflict (as reflected in subordinate glucocorticoid levels) may be elevated with increased group size in such species, though it does not distinguish whether this is due to conflict with dominants or other subordinates.

Our results emphasize that conflict among subordinates may be a strong cause of variation in subordinate glucocorticoid levels as is conflict between dominants and subordinates. Furthermore, our study highlights the importance of simultaneously considering how individual, social, and environmental factors affect subordinate glucocorticoid levels. Future studies should consider how multiple causes of intra-group conflict affects subordinate glucocorticoid levels and how this conflict can be ameliorated when subordinates experience benign environmental conditions or high food availability.

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