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Original Article

Effects of cortisol administration on cooperative behavior in meerkat helpers

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Although the ultimate causes for variation in contributions to helping in cooperative breeders are increasingly well understood, the underlying physiological mechanisms remain largely unknown. Recent work has suggested that glucocorticoids may play an important role in the expression of cooperative behavior. Here, we present the first experimental test of the effects of glucocorticoids on helper behavior in a cooperative breeder. Glucocorticoid levels of adult female and male meerkat, *Suricata suricatta*, helpers were elevated with an intramuscular injection of cortisol (hydrocortisone 21-hemisuccinate sodium salt) dissolved in saline, whereas matched controls simultaneously received an injection of physiological saline. The treatment successfully elevated circulating glucocorticoid levels but did not result in significant changes in pup feeding or sentinel behavior. Females, however, spent less time foraging when glucocorticoid levels were elevated and appeared to spend more time in close proximity to pups. These results provide no evidence that glucocorticoids affect cooperative behaviors but suggest that there may be an effect on foraging effort and affiliation with pups.

Key words: cooperative breeding, cortisol, helpers, stress hormones, *Suricata suricatta*.

INTRODUCTION

One remaining challenge in the study of cooperative breeding is to understand why individuals vary in their contributions to cooperative activities (Komdeur 2006). Although the ultimate causes underlying this variation are increasingly well understood and have been shown to be associated with factors such as sex, age, condition, and relatedness to offspring (e.g., Komdeur 2006; West et al. 2007), the underlying physiological mechanisms remain largely unknown. Initial studies examining a physiological basis for cooperative behavior focused primarily on the hormones prolactin and testosterone (Schoech et al. 2004), but recently the role of glucocorticoids (GCs) has attracted more attention (Soares et al. 2010). GCs are a class of hormones, produced by activation of the hypothalamic–pituitary–adrenal axis in response to stressors, of which cortisol is the primary type in mammals (Sapolsky et al. 2000; Landys et al. 2006).

Recent work on cooperative breeders has suggested that GCs may be an important factor underlying individual variation in contributions to cooperative activities. In subordinate male meerkats (*Suricata suricatta*), pup provisioning rates were positively correlated

with GC levels at the start of the breeding attempt (Carlson et al. 2006), and meerkat males who were frequently on sentinel duty had higher GC levels than those who were infrequently on sentinel duty (Tatalovic 2008). Such increases in contributions to cooperative activities may result directly from the effects of GCs on cooperative behavior or indirectly from the effects of GCs on foraging rates and food intake (Koch et al. 2002; Dallman et al. 2004), attention and vigilance (Chapotot et al. 1998), and interactions with offspring (Fleming et al. 1997), which may facilitate cooperative behavior. To date, however, no studies have experimentally tested the effects of GCs on behavior of helpers in cooperative breeders, and it remains unclear whether previously reported correlations between GC levels and contributions to cooperative activities represent a causal link.

Our aim was to examine the effects of elevated GC levels on contributions to pup feeding and sentinel behavior, as well as on foraging, vigilance, and affiliation with pups. Meerkats live in groups of up to 50 individuals with a dominant breeding pair that largely monopolizes reproduction and helpers of both sexes who do not normally breed (Griffin et al. 2003). Litters of up to 7 pups are produced 2–4 times per year by the dominant pair and raised cooperatively by the group (Clutton-Brock, Gaynor, et al. 1999). Typically, the group leaves the sleeping burrow after sunrise

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to forage for the day and returns to the burrow around sunset. During these foraging trips, helpers engage in 2 distinct forms of cooperative behavior. First, when dependent pups are present in the group, adults provision them with invertebrate and small vertebrate prey items, a behavior referred to as “pup feeding” (Clutton-Brock et al. 2002, 2003; Santema and Clutton-Brock 2012). Second, group members occasionally cease foraging to scan for predators from an elevated position and to alert the group when detecting a predator, a behavior referred to as “sentinel duty” (Clutton-Brock, O’Riain, et al. 1999; Santema and Clutton-Brock 2013).

We first validated the use of intramuscular injection of cortisol as a method to elevate circulating GC levels in meerkats. We then used this method to elevate GC levels of meerkat helpers to test its effects on pup feeding, sentinel behavior, foraging, vigilance, and association with pups by conducting 80-min observations, starting 15 min after the injections. In addition, 2 h after the injections, an experiment was performed where food items were provided to the focal individuals, in order to specifically test the effects of elevated GC levels on pup feeding behavior.

METHODS

Study site and population

The study was conducted in the southern Kalahari Desert, South Africa (26°58’S, 21°49’E). The ecological conditions and climate of the study site have been described elsewhere (Clutton-Brock, Gaynor, et al. 1999; Clutton-Brock, Maccoll, et al. 1999; Russell et al. 2002). All meerkats in the study population are habituated to human presence and can be identified by a unique pattern of dye marks on their fur. Dominance status of males and females can be readily identified, as subordinate helpers are behaviorally submissive to the dominants (Clutton-Brock, Maccoll, et al. 1999). Groups are visited at least once every 3 days and the age of all individuals is therefore known to within a few days. Individuals are referred to as pups until they reach 90 days of age and able to forage independently and as adults after they reach 12 months of age and have the potential to reproduce (Brotherton et al. 2001).

GC treatment validation

In May 2010 and May 2011, trials were performed to examine the effects of intramuscular injection of cortisol on circulating GC levels. For the treatment, 3 adult male helpers and 2 adult female helpers received an injection of 10 mg cortisol (hydrocortisone 21-hemisuccinate sodium salt, Sigma–Aldrich, Buchs, Switzerland) dissolved in 0.05 mL physiological saline solution. For the control, 4 adult male helpers and 2 adult female helpers received an injection of 0.05 mL saline solution only. We administered injections intramuscularly in the thigh of meerkats, using a 1-mL syringe with a 25-G needle, which could be done when they were sunning themselves without the need to capture or restrain them (Madden and Clutton-Brock 2011). The physiological and functional effects of exogenous hydrocortisone 21-hemisuccinate sodium salt administration have previously been demonstrated in various mammal species. In common marmosets, intramuscular injection increased circulating GC levels and triggered changes in maternal behavior (Saltzman and Abbott 2009), whereas oral administration in Belding’s ground squirrels (*Spermophilus beldingi*) resulted in elevated fecal GC values and reduced performance at memory tests. In squirrel monkeys (*Saimiri sciureus*), oral administration increased circulating GC levels and both oral and intramuscular administration affected their cognitive performance (Lyons et al. 2000, 2004).

Two hours (mean: 121 min \pm 4.3 standard error [SE]) after the injection, a blood sample was taken for subsequent analyses of serum GC levels. For this, meerkats were captured by gently lifting them by the tail base, placing them in a cotton bag, and carrying them to a nearby vehicle (Jordan et al. 2007). Anesthesia was induced immediately by placing a small “gas mask” over the meerkat’s nose and delivering a dose of 4% isoflurane (Isofor; Safe Line Pharmaceuticals, Johannesburg, South Africa) from a portable, car-mounted vaporizer, using oxygen as a vehicle at a flow rate of 4L/min (Jordan et al. 2007). When fully sedated, anesthesia was maintained with a reduced isoflurane dose of 1–2% until blood sampling was completed (Jordan et al. 2007). Blood (0.5–1.5 mL) was drawn from the jugular vein using a 25G needle and a 2-mL syringe (Drewe 2009). All blood samples were collected within 5 min from the moment of capture (mean: 3.36 min \pm 1.03 standard deviation [SD]) and 60% of the samples were collected within 3 min from the moment of capture. These are among the shortest capture-to-bleed times for free-living mammals, therefore minimizing the potential effects of capture stress on circulating GC levels (Schoech et al. 1996; Romero and Reed 2005). Capture-to-bleed times were comparable for individuals that received an injection of cortisol (mean: 3.40 min \pm 0.54 SD) and individuals that received an injection of saline (mean: 3.33 min \pm 1.37 SD). Following sampling, meerkats were placed in a recovery box and regained normal locomotory ability after 1–7 min, after which they were released back into the group (Jordan et al. 2007). They invariably resumed their normal foraging behavior within 1–3 min following release and were then observed for another 10 min to ensure there were no adverse effects.

Blood samples were kept cool on wet ice until they were centrifuged at the research station within 1 h. Serum was pipetted off and frozen at -20°C . Serum samples were then shipped to the University of Pretoria where they were analyzed for GC levels using a coat-a-count cortisol kit (Diagnostic Products Corporation). A series of known calibrators of cortisol were assayed to set up a standard curve. Serum samples (25 μL) and ^{125}I -labelled cortisol (1000 μL) were added to assay tubes in duplicate and briefly vortexed. Assay tubes were then incubated in a water bath (37 $^{\circ}\text{C}$) for 45 min. Bound and free ^{125}I -labelled cortisol were separated by decanting the excess label from the assay tubes, which were then counted in a gamma counter for 1 min. A calibration curve was used to convert the counts into cortisol concentrations. A serial double dilution of a sample containing a high concentration of cortisol paralleled the standard curve, validating the assay (ANCOVA, $F = 1.34$, $P < 0.05$). The sensitivity of the assay was 5.5 nmol/L, and the intra-assay coefficient of variation was 7.0%. The assay has previously been validated for use in meerkats by Carlson et al. (2004).

Experimental protocol

All trials were carried out when pups between 40 and 75 days of age were present in the group, between October 2011 and March 2012. We selected 2 same-sex adult littermates and randomly assigned one to receive an injection of 10 mg cortisol dissolved in 0.05 mL physiological saline and the other to receive an injection of 0.05 mL saline only. For 2 of the trials, no 2 same-sex littermates were available, and 2 individuals of the same sex and an age difference of no more than 6 months were selected. Injections were performed while the meerkats were sunning in the morning before leaving the burrow to forage. The observers were blind to the treatment being applied, such that the person performing the injections did not know which treatment was being administered, and the observers did not know which individual had received what treatment (Madden

and Clutton-Brock 2011). Both focal individuals were subsequently observed simultaneously with 2 observers (see below) such that any behavioral variation due to environmental factors or diurnal patterns was eliminated. In total, 24 trials were performed on 12 female pairs and 12 male pairs in 8 different groups.

Behavioral observations started 15 min after the injections, or, if the group was not foraging yet after 15 min, as soon as the group started foraging. This resulted in an average of 26 (± 2 SE) min between the injections and the onset of the observations. Four 20-min continuous focal observations (Altmann 1974) were performed on both meerkats simultaneously, with 2 observers, resulting in a total observation time of 80 min for each individual. To avoid observer bias, the observers switched between focal individual after each 20-min observation. Behavioral data were entered directly onto a handheld Psion organizer (Psion Teklogix Inc., Ontario, Canada), programmed as a data logger that allows recording of behaviors to the nearest second. During focal observations, all food items found, including their size category and whether or not they were fed to a pup, were recorded, as well as all instances of sentinel behavior. In addition, the amount of time spent foraging, the amount of time spent within 2 m of a pup, and the number of times on bipedal vigilance were recorded. An individual was regarded to be on bipedal vigilance when it interrupted foraging to adopt a bipedal position to scan the environment, typically lasting a few seconds. Following previous studies, food items were categorized as tiny, small, medium, or large. The biomass was then estimated using the average mass of the food items in each size category (tiny = 0.05 g, small = 0.11 g, medium = 0.58 g, and large = 2.86 g; Thornton 2008). Observations were paused if foraging was interrupted for more than 1 min (e.g. by alarm calls) and continued when foraging had been resumed by at least 50% of the group.

Scorpion provisioning

In order to specifically test the effects of elevated GC levels on pup feeding behavior, an additional experiment was performed where scorpions (*Opisthophthalmus* sp.) were supplementarily provisioned. Scorpions, which are part of the meerkat's natural diet, are common in the area and frequently fed to pups (Thornton and McAuliffe 2006). Starting 2 h (mean: 128 min \pm 3 SE) after the injections, 4 scorpions were sequentially presented (at 5-min intervals) to each of the 2 focal individuals ($N = 12$ males and 12 females, each with a matched control). Scorpions were presented while meerkats were digging a foraging hole in order to ensure they did not see that it was provided by the experimenter. Presentations were performed when no other meerkat was within 2 m, to avoid potential interruption by other individuals, and when pups were begging within audible distance. For each individual, we recorded how many out of the 4 presented scorpions were fed to a pup.

Ethical note

Preliminary trials of intramuscular injections of cortisol and saline were conducted on a small number of individuals. When these trials revealed no harmful effects and showed that circulating GC levels were successfully elevated, we commenced the experiment on a larger number of individuals. The amount of cortisol administered was based on published work on common marmosets, where 40 mg cortisol was injected per kilogram of body weight (Saltzman and Abbott 2009). Corrected for the body weight of meerkat helpers (~700 g), the dosage in our study represents approximately a third of the dosage used in marmosets. All injections were performed

when meerkats were sunning themselves in the morning. Meerkats typically sprang away from the injections but resumed sunning within seconds and did not become wary toward the experimenters. They responded in a similar manner to bites of ants that they naturally encounter (Madden and Clutton-Brock 2011; Santema P, personal observation). Following the treatments, we continued observing the meerkats as part of the ongoing study on the population, and no long-term abnormalities in their behaviors or response to human observers were noted nor were there any infections or injuries.

RESULTS

GC treatment validation

Individuals that received an injection of 10 mg cortisol dissolved in saline ($N = 3$ males and 2 females) had an average of 296.6 (± 187.3 SD) ng GC/mL serum 2 h after the injection, whereas individuals that received an injection of saline only ($N = 4$ males and 2 females) had an average of 28.1 (± 34.0 SD) ng GC/mL serum (Figure 1). To test whether cortisol and saline injection led to changes in circulating GC levels, we compared them against 22 untreated individuals (21 males and 1 female) that were measured as part of an earlier study (mean \pm SD = 51.3 \pm 37.5 ng GC/mL serum; Santema P, unpublished data; Figure 1). GC levels of individuals that received an injection of cortisol were significantly higher than GC levels of untreated individuals (Mann–Whitney U test: $V = 13$, $N_1 = 5$, $N_2 = 22$, $P = 0.010$). GC levels of individuals that received an injection of saline solution were not significantly different from GC levels of untreated individuals (Mann–Whitney U test: $V = 94$, $N_1 = 6$, $N_2 = 22$, $P = 0.12$). Finally, direct comparison showed that individuals injected with cortisol had significantly higher GC levels than those injected with saline (Mann–Whitney U test: $V = 28$, $N_1 = 5$, $N_2 = 6$, $P = 0.022$).

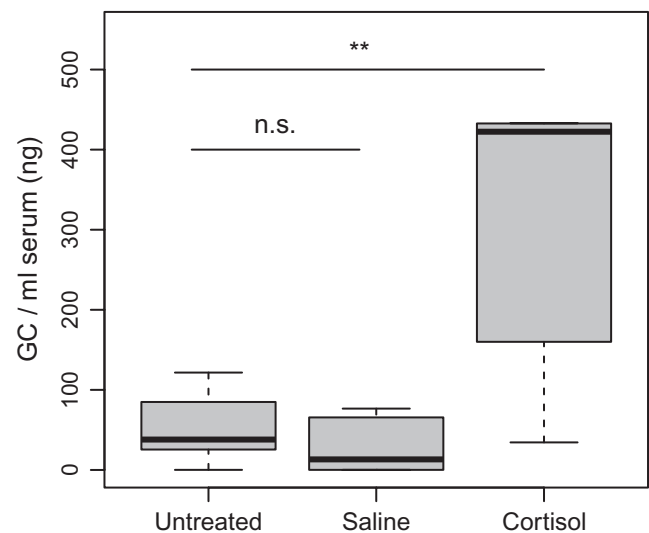


Figure 1

Serum GC levels of untreated meerkat helpers ($N = 21$ males and 1 female), meerkat helpers that were injected with saline solution only ($N = 4$ males and 2 females), and meerkat helpers that were injected with 10 mg cortisol dissolved in saline solution ($N = 3$ males and 2 females). Figures represent medians, IQ intervals, and ranges. $**P < 0.01$.

Behavioral observations

Intramuscular cortisol administration had no significant effect on the total biomass that was fed to pups by females (exact Wilcoxon signed-rank test: $N = 12, V = 36, P = 0.41$; Figure 2a) or by males (exact Wilcoxon signed-rank test: $N = 12, V = 17.5, P = 0.59$; Figure 2a) nor on the proportion of biomass that was fed to pups relative to the amount of biomass found by females (exact Wilcoxon signed-rank test: $N = 12, V = 42, P = 0.45$) or by males (exact Wilcoxon signed-rank test: $N = 12, V = 24, P = 0.76$). Cortisol administration had no significant effect on the number of times individuals went on sentinel duty in females (exact Wilcoxon signed-rank test: $N = 12, V = 5, P = 1$; Figure 2b) or in males (exact Wilcoxon signed-rank test: $N = 12, V = 27.5, P = 0.20$; Figure 2b).

Cortisol administration resulted in a reduction in the amount of time spent foraging by females (exact Wilcoxon signed-rank test: $N = 12, V = 1, P < 0.001$; Figure 2c) but not by males (exact Wilcoxon signed-rank test: $N = 12, V = 30, P = 0.52$; Figure 2c). Cortisol administration did not, however, affect the total biomass found by females (exact Wilcoxon signed-rank test: $N = 12, V = 46, P = 0.62$; Figure 2d) or by males (exact Wilcoxon signed-rank test: $N = 12, V = 29, P = 0.47$; Figure 2d) or the frequency of bipedal vigilance by females (exact Wilcoxon signed-rank test: $N = 12, V = 29, P = 0.76$; Figure 2e) or by males (exact Wilcoxon

signed-rank test: $N = 12, V = 31.5, P = 0.93$; Figure 2e). Finally, cortisol increased the amount of time spent within 2 m of pups by females (exact Wilcoxon signed-rank test: $N = 12, V = 68, P = 0.021$; Figure 2f), but not by males (exact Wilcoxon signed-rank test: $N = 12, V = 43, P = 0.79$; Figure 2f).

Scorpion provisioning

Female helpers that were injected with cortisol fed on average more scorpions to pups than female helpers that were injected with saline solution, though this difference was not statistically significant (exact Wilcoxon signed-rank test: $N = 12, V = 13.5, P = 0.59$; Figure 3). Male helpers that were injected with cortisol also fed on average more scorpions to pups than male helpers that were injected with saline solution, but this difference was also not statistically significant (exact Wilcoxon signed-rank test: $N = 12, V = 19, P = 0.44$; Figure 3).

DISCUSSION

We provide the first experimental test of the effects of GCs on helping behavior in a cooperative breeder. Intramuscular injections of cortisol successfully elevated circulating GC levels in meerkat helpers but did not significantly affect contributions to pup feeding or

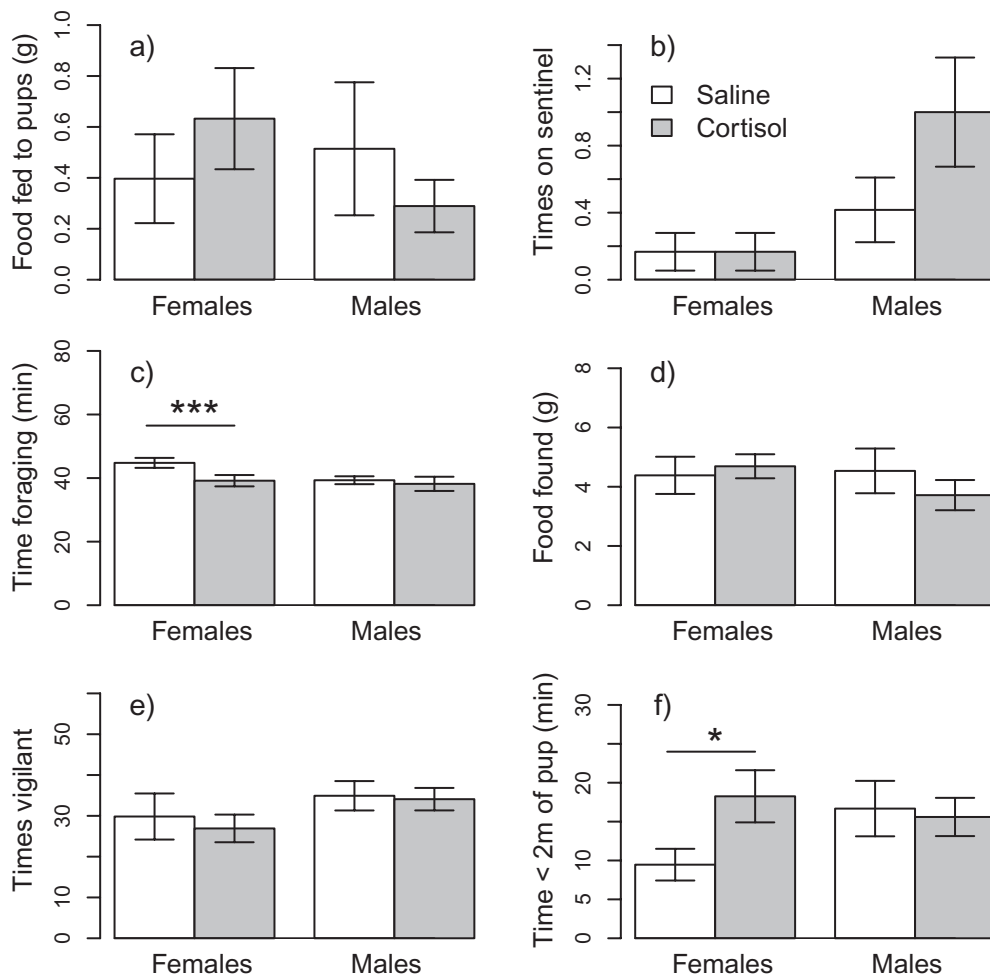


Figure 2 Effects of intramuscular cortisol administration on (a) amount of food given to pups, (b) sentinel behavior, (c) time spent foraging, (d) amount of food found, (e) bipedal vigilance, and (f) time spent near pups. Figures represent mean per 80 min observation \pm SE. * $P < 0.05$ and *** $P < 0.001$.

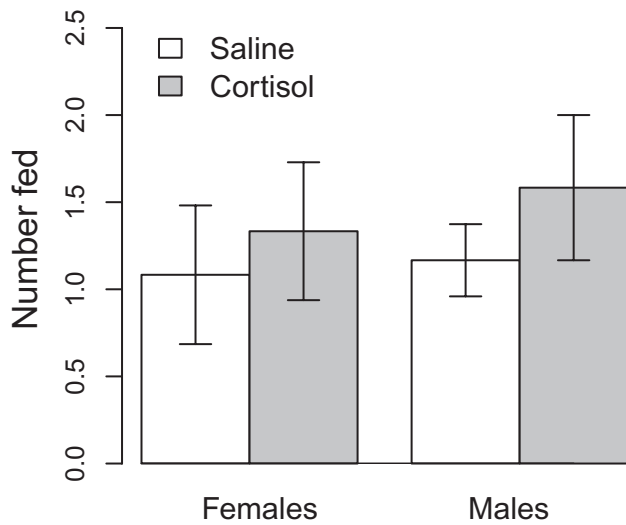


Figure 3
Effects of intramuscular cortisol administration on the number of scorpions given to a pup out of a total of 4 provisioned scorpions. Figures represent mean \pm SE.

sentinel behavior by either females or males. Also, when scorpions were experimentally provisioned, the number that was fed to pups was not significantly affected by cortisol administration for either females or males. Females did, however, show a decrease in the time spent foraging and an increase in the time spent close to pups when injected with cortisol. Males did not show changes in either the time spent foraging or the time spent close to pups. Finally, cortisol administration did not affect the amount of food found or the frequency of bipedal vigilance by either females or males.

The longer time spent in close proximity to pups may result either from cortisol-treated females seeking the vicinity of pups or vice versa. Previous work on meerkats suggests that pup-helper associations result primarily from the behavior of pups (Hodge et al. 2007), indicating that our result may arise from pups that actively seek the vicinity of cortisol-treated females, perhaps because they are more easy to follow because of their less active foraging behavior. The functional significance of the increased time spent in close proximity to pups by females treated with cortisol remains unclear, however, as cortisol-treated females do not have higher pup feeding or guarding rates. Pups may nevertheless have benefited from this association through factors that we did not measure, such as increased protection from predators. However, the spacing effect was only marginally significant, cautioning against overinterpretation of this result, especially in the light of the multiple hypothesis tested in this study.

Our results do not confirm previous findings that GCs affect contributions to cooperative activities in meerkat helpers (Carlson et al. 2006; Tatalovic 2008). Although there was a tendency for males to perform more sentinel behavior, for females to perform more pup feeds when injected with cortisol, and for both males and females to perform more pup feeds when scorpions were experimentally provisioned, these trends were not statistically significant. Previous studies on the effects of GCs on cooperative and prosocial behavior have also reported diverse results. GC levels were unrelated to contributions to cooperative offspring care in the cooperatively breeding cichlid *Neolamprologus pulcher* (Bender et al. 2008) and to infant carrying by male helpers and fathers in the cooperatively breeding cotton top tamarin (*Saguinus oedipus*,

da Silva Mota et al. 2006). Among noncooperative breeders, various effects of GC levels on offspring care have also been reported. For instance, human mothers with higher GC levels showed more affectionate behavior toward offspring and were more responsive to infant cries (Fleming et al. 1987, 1997), whereas western lowland gorilla (*Gorilla gorilla*) and savannah baboon (*Papio hamadryas*) mothers with higher GC levels spent less time in contact with their infants (Bahr et al. 1998; Bardi et al. 2004), and common marmoset mothers carried their infants less when GC levels were experimentally elevated (Saltzman and Abbott 2009). Also, in contrast to our finding that females spent less time foraging when GC levels were experimentally elevated, foraging effort and food intake were found to increase after experimental elevation of GC levels in ring doves (*Streptopelia risoria*, Koch et al. 2002), and GC levels were shown to be positively associated with food intake in humans (Dallman et al. 2004).

The most obvious conclusion from this brief overview is that there is little consistency in the effects of GCs on cooperative or caregiving behavior. Indeed, previous work suggests that behavioral responses to GC elevation may depend on a range of factors. First, experiences earlier in life may affect behavioral responses to GC elevation. For example, female rats with reproductive experience showed increased maternal behavior in response to GC elevation, whereas virgin females showed a reduction in maternal behavior (Rees et al. 2004, 2006). Second, life-history characteristics of a species may affect behavioral responses to GC elevation. For instance, GC elevation may affect breeding behavior in nonseasonal species with flexible timing of breeding but not in highly seasonal species with only a short window of opportunity for breeding (Wingfield and Sapolsky 2003). Third, GC elevation may have divergent behavioral effects depending on the duration of GC elevation and the level of increase (Sapolsky 1992), and relations between GC levels and behavioral responses may be nonlinear and even inverted U shaped (Mateo 2008). These complexities in the relationship between GC levels and the expression of behavior make it difficult to make generalizations about the behavioral effects of GCs across different contexts. Future work may therefore benefit from more targeted experiments under controlled conditions in order to unravel the behavioral effects of GCs.

In summary, we successfully elevated circulating GC levels in meerkat helpers using intramuscular injections, but this had no significant effect on pup feeding or sentinel behavior by either females or males. Females, however, spent more time in close proximity to pups and less time foraging when GC levels were elevated. Males showed no behavioral changes in response to GC elevation. These results suggest that affiliation with pups and foraging effort may be affected by GC levels but that these effects may be sex specific. The available evidence from different species, however, suggests that behavioral responses to GC elevation may be affected by a range of factors, and more targeted experiments are needed to illuminate the complex relations between GCs and the expression of cooperative behavior.

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