

1 **Maternal stress increases cooperative behaviour of offspring in wild meerkats**

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18

19 **Abstract**

20 The phenotype of parents can have long-lasting effects on the development of offspring  
21 as well as on their behaviour, physiology, and morphology as adults. In some cases,  
22 these changes may increase offspring fitness but, in others, they can elevate parental  
23 fitness at a cost to the fitness of their offspring. Here, we show that in Kalahari meerkats  
24 (*Suricata suricatta*) the circulating glucocorticoid hormones of pregnant females affect  
25 the growth and cooperative behaviour of their offspring. We performed a 3-year  
26 experiment in wild meerkats to test the hypothesis that stress-mediated maternal effects  
27 reduce the potential for offspring to reproduce directly and therefore cause them to  
28 exhibit more cooperative behaviour. Daughters (but not sons) born to mothers treated  
29 with cortisol during pregnancy were smaller early in life and exhibited significantly more  
30 of two types of cooperative behaviour (pup rearing and feeding) once they were adults  
31 compared to offspring from control mothers. They also had lower measures of stress  
32 hormones as they aged, which could explain the observed increases in cooperative  
33 behaviour. Because early growth is a crucial determinant of fitness in female meerkats,  
34 our results indicate that stress-mediated maternal effects may reduce the fitness of  
35 offspring but may elevate parental fitness as a consequence of increasing the  
36 cooperative behaviour of their daughters.

37 **Significance Statement**

38

39 Maternal characteristics can have a profound influence on offspring, which are referred  
40 to as maternal effects. It is widely assumed that selfish maternal effects, where mothers  
41 modify offspring to benefit their own fitness and decrease the fitness of offspring, are  
42 rare but this assumption is rarely tested. We show that a stress-mediated maternal  
43 effect in meerkats altered the growth, behaviour, and stress physiology of daughters in  
44 such a way that benefitted mothers at the expense of their daughters. Daughters from  
45 stressed mothers grew more slowly early in life, which should reduce their future  
46 reproductive opportunities, but exhibited more cooperative behaviour that should  
47 directly benefit their mother. This highlights the important role of sociality in the  
48 evolution of maternal effects.

49

## 50 **Introduction**

51 Parental effects are a mechanism of trans-generational phenotypic plasticity that  
52 occurs when the parental phenotype or parental environment modifies offspring  
53 characteristics (1). Parental effects can increase the survival or reproduction of  
54 offspring, thereby elevating the direct fitness of both offspring and parents (2-6).  
55 Alternatively, parental effects can increase parental fitness, but at some cost to the  
56 fitness of their offspring (7-8) – a process regarded as a type of parental manipulation  
57 (9-12) or ‘selfish parental effect’ (13). For example, in mammals, the optimal birth weight  
58 or litter size often differs between mothers and offspring (14) and pregnant females  
59 experiencing stressful environments may reallocate resources away from offspring and  
60 towards themselves, so that their offspring are smaller or grow more slowly before  
61 weaning (15). Despite these observations, it has also been suggested that selfish  
62 parental effects may be rare and unstable because selection would be expected to  
63 favour the evolution of resistance mechanisms in offspring (7, 11, 13, 16, 17).

64 Selfish parental effects may in fact be more likely in cooperatively breeding  
65 species where philopatric offspring (subordinates) help to rear the subsequent offspring  
66 of their parents or other close relatives. This is because parents may gain substantial  
67 direct fitness benefits from delaying the development of their offspring if this causes  
68 them to invest in alloparental care directed at the parent’s subsequent offspring (9-10).  
69 In addition, the costs of selfish parental effects to offspring could be reduced in these  
70 circumstances, as offspring will gain indirect fitness benefits by contributing to raising  
71 the subsequent offspring of their parents (18). For example, laboratory studies of  
72 eusocial insects suggest the possibility that selection will favour the evolution of alleles

73 that enable mothers to increase the helping behaviour of their offspring while  
74 simultaneously reducing their capabilities of reproducing on their own (19-20; but see  
75 21). In addition, it is often the case that the probability that parents will rear young  
76 successfully is substantially higher than the probability that inexperienced and  
77 subordinate females will do so, increasing the inclusive fitness benefits of helping  
78 versus breeding to offspring (22).

79 To date, empirical field tests of how parental effects shape the helping behaviour  
80 of offspring are rare (23) and studies of selfish parental effects have mostly focused on  
81 non-social species (13, 24). Here, we report the results of experiments designed to test  
82 the hypothesis that elevated maternal glucocorticoid (stress hormone) levels reduce the  
83 potential for offspring to have direct reproductive opportunities and causes them to  
84 exhibit more cooperative behaviour. In a 3-year field study, we experimentally elevated  
85 maternal stress by treating pregnant dominant female meerkats with glucocorticoids  
86 (cortisol) and tracking the growth, stress physiology, and cooperative behaviour of their  
87 offspring from birth until ~18 months of age, compared to those from control litters. We  
88 manipulated maternal glucocorticoids because they are known to cause mothers to  
89 reallocate energy away from offspring and towards themselves (15), indicating that they  
90 may function as a mediator of selfish maternal effects. Changes in maternal  
91 glucocorticoids have also previously been shown to delay the dispersal of offspring as  
92 well as influence the parental care behaviour of offspring (25-26), both traits that are  
93 important in cooperative breeders where philopatric offspring exhibit alloparental care  
94 behaviour towards juveniles.

95 To identify if the exposure of mothers to heightened glucocorticoids reduced  
96 reproductive success of their offspring, we examined if offspring from mothers treated  
97 with cortisol during pregnancy grew slower or were smaller early in life. In meerkats, the  
98 rate of early life growth and body mass is closely linked to future direct fitness through  
99 its effects on survival, foraging success, adult body mass (27-29), as well as the  
100 probability of acquiring dominance (30-31) and other direct reproductive opportunities  
101 (32). As elevated exposure to maternal glucocorticoids in some mammals may reduce  
102 offspring size and growth early in life (15), we predicted that offspring from mothers  
103 treated with cortisol during pregnancy would be smaller early in life and would  
104 consequently contribute more to cooperative activities than controls.

105 Secondly, we determined if offspring from mothers treated with cortisol during  
106 pregnancy subsequently increased their contributions to two types of cooperative  
107 behaviours: pup rearing (“babysitting”: 33) and food provisioning during the period when  
108 the pups are foraging with their natal group but are not yet nutritionally independent  
109 (“pup feeding”: 34). If offspring from mothers treated with cortisol during pregnancy  
110 exhibit more of either of these two types of alloparental care, this should increase both  
111 parental fitness and the indirect fitness of offspring because subsequent offspring that  
112 receive more alloparental care should grow faster or have higher early life survival (27,  
113 32, 35, 36).

114 To assess the mechanism by which elevated exposure to maternal stress may  
115 affect the alloparental care behaviour of offspring, we repeatedly measured plasma  
116 cortisol and faecal glucocorticoid metabolite (fGCM) concentrations of offspring from  
117 when they were approximately 1 to 18 months of age to identify how our manipulations

118 affected their neuroendocrine stress axes (glucocorticoid output). Elevated maternal  
119 glucocorticoids can cause long-term changes in the neuroendocrine stress axis of  
120 offspring (37) and elevated activity of the neuroendocrine stress axis in meerkats can  
121 reduce their contributions to alloparental care (38). We therefore predicted that if  
122 offspring born to mothers treated with cortisol during pregnancy exhibited more  
123 alloparental care behaviour compared to controls, they would also have reduced plasma  
124 cortisol and fGCM concentrations.

125

## 126 **Results**

### 127 *Effects of treatments on litter characteristics and offspring survival*

128 There was no evidence that the treatment of pregnant females with cortisol  
129 affected their ability to maintain litters to term or the survival of their pups prior to  
130 emergence from the natal burrow (Tables S1-S2). The number of pups surviving to  
131 emergence from the natal burrow or 3, 6, or 12 months of age and the litter sex ratio  
132 were not different among litters from cortisol-treated (31 pups from 10 litters produced  
133 by 9 dominant females), control (25 pups from 6 litters produced by 6 females), or  
134 untreated (195 pups from 52 litters produced by 21 dominant females) females (Table  
135 S1-S2).

### 136 *Effects of treatments on offspring early life body mass*

137 The effects of the treatments on body mass from initial emergence to nutritional  
138 independence (1-3 months) differed between daughters and sons and depended upon  
139 the age of offspring (Table S3). Daughters (but not sons) from cortisol treated litters  
140 were significantly smaller from 1-3 months than those from control litters especially as

141 they approached nutritional independence (daughters: age  $\times$  treatment,  $t = -4.17$ ,  $P <$   
142  $0.0001$ ; sons:  $t = -1.48$ ,  $P = 0.14$ ), but were of similar body mass compared to those  
143 from untreated litters (daughters: age  $\times$  treatment,  $t = 0.65$ ,  $P = 0.51$ ; sons:  $t = -0.52$ ,  $P$   
144  $= 0.6$ , Table S3, Fig. 1). This difference in body mass between daughters from mothers  
145 treated with cortisol during pregnancy and those from control litters increased from one  
146 to three months, as indicated by the significant interaction between age and control  
147 treatment (Table S3). Daughters, but not sons, from control litters were larger than  
148 those from untreated litters, especially as they got older (daughters: age  $\times$  treatment,  $t =$   
149  $-4.24$ ,  $P < 0.0001$ ; sons:  $t = 1.35$ ,  $P = 0.18$ ).

#### 150 *Effects of treatments on offspring cooperative behaviour*

151 The effects of the maternal treatments on babysitting behaviour of offspring  
152 depended upon the age and sex of the offspring (Table S4). Babysitting contributions in  
153 daughters from mothers treated with cortisol during pregnancy slightly, but significantly  
154 increased and rose more rapidly with increasing age of the babysitter than those from  
155 control litters (age  $\times$  treatment,  $z = -2.89$ ,  $P = 0.0039$ ) but not untreated litters (age  $\times$   
156 treatment,  $z = 1.88$ ,  $P = 0.06$ ; Table S4, Fig. 2). Babysitting contributions in sons from  
157 mothers treated with cortisol during pregnancy showed a similar tendency to slightly  
158 increase more rapidly with age compared to those from control litters, but this difference  
159 was not significant (age  $\times$  treatment,  $z = -1.92$ ,  $P = 0.055$ ). Further, age-related  
160 increases in babysitting contributions between males from mothers treated with cortisol  
161 during pregnancy and untreated litters did not differ (age  $\times$  treatment,  $z = -0.03$ ,  $P =$   
162  $0.97$ ; Table S4, Fig. 2). Comparisons of the magnitude of effect sizes showed that the  
163 interaction between age and litter treatment had a larger effect on babysitting

164 contributions in daughters but not sons than other variables known to impact babysitting  
165 contributions, such as foraging success, age-related body mass, or group size (Table  
166 S4).

167         The effects of the maternal treatments on pup feeding depended upon the sex of  
168 the offspring, but not their age (Table S5). Daughters but not sons from mothers treated  
169 with cortisol during pregnancy exhibited significantly more pup feeding contributions  
170 than those from control litters (females:  $z = -3.12$ ,  $P = 0.00018$ ; males:  $z = -1.14$ ,  $P =$   
171  $0.25$ ) or untreated litters (females:  $z = -3.49$ ,  $P = 0.0005$ , sons:  $z = -1.03$ ,  $P = 0.3$ , Table  
172 S5, Fig. 3). Notably, the magnitude of effect size of litter treatment for daughters was  
173 much larger than other variables known to impact babysitting contributions such as  
174 foraging success, age-related body mass, and group size (Table S5).

#### 175                 *Effects of treatments on offspring stress physiology*

176         Daughters and sons from mothers treated with cortisol during pregnancy had  
177 lower plasma cortisol and fGCM concentrations as they became older compared to  
178 those from control litters. Plasma cortisol concentrations in daughters from mothers  
179 treated with cortisol during pregnancy had lower plasma cortisol concentrations as they  
180 became older compared to those from control litters but these differences were not  
181 significant (age  $\times$  treatment,  $t = -1.61$ ,  $P = 0.11$ , Table S6, Fig. 3A). fGCM  
182 concentrations in daughters were significantly lower than those from control litters as  
183 they became older (age  $\times$  treatment,  $t = -2.95$ ,  $P = 0.0033$ , Table S7, Fig. 4A). Sons  
184 from mothers treated with cortisol during pregnancy had significantly lower plasma  
185 cortisol concentrations as they became older compared to those from control litters (age  
186  $\times$  treatment  $t = -2.59$ ,  $P = 0.01$ , Table S6, Fig. 3B) but similar fGCM concentrations

187 compared to those from control litters as they became older (age  $\times$  treatment,  $t = -0.49$ ,  
188  $P = 0.62$ , Table S7, Fig. 4B).

189

## 190 **Discussion**

191 We found some support for our hypothesis that elevated maternal stress would  
192 reduce the potential for offspring to have direct reproductive opportunities and would  
193 therefore shift them towards exhibiting more cooperative behaviour that should increase  
194 their indirect fitness. Daughters, but not sons, from mothers treated with cortisol during  
195 pregnancy grew more slowly early in life and exhibited more babysitting and pup  
196 feeding behaviour as they became older compared to controls. Other than offspring  
197 survival (Table S2), we were unable to quantify the direct and indirect fitness of  
198 offspring from control or cortisol-treated litters, but early life growth or body mass (which  
199 we measured here) is closely linked to direct fitness opportunities in daughters.

200 Previous studies in meerkats show that female, but not male, offspring that grow faster  
201 from 1-3 months are more likely to acquire the dominant breeding position (31), perhaps  
202 because offspring that grow faster from 1-3 months are heavier later in life (32, 39, 40),  
203 and heavier females are more likely to acquire a vacant dominant breeding position (30,  
204 32). As such, daughters, but not sons, from mothers with elevated cortisol levels during  
205 pregnancy should have reduced future direct fitness opportunities and therefore  
206 increase their investment in behaviours that elevate their indirect fitness. Our results are  
207 consistent with studies in other taxa that suggest that individuals adjust their  
208 contributions to cooperative behaviour according to their future reproductive potential.  
209 For example, wasps whose probability of acquiring the dominant breeding position was

210 experimentally increased exhibited significantly less helping behaviour (41). Similarly, in  
211 cooperatively breeding fish, subordinates will reduce their helping investment  
212 immediately prior to dispersal from their natal group where they attempt to reproduce on  
213 their own rather than stay in their natal group and queue for dominance (42).

214         The effects of maternal stress on offspring should lead to substantial fitness  
215 benefits to mothers. Daughters from mothers treated with cortisol during pregnancy  
216 exhibited more alloparental care compared to controls, such that subsequent offspring  
217 produced in groups with offspring from cortisol-treated litters should have received more  
218 alloparental care behaviours. Because offspring that receive more alloparental care  
219 grow faster early in life or are larger later in life (32, 39), the presence of offspring from  
220 cortisol-treated litters should increase the direct fitness of dominant breeders and the  
221 indirect fitness of the cortisol-treated offspring. Taken together, our results suggest that  
222 this stress-mediated maternal effect reduced the direct fitness opportunities of  
223 daughters by reducing their early life growth but they compensated by increasing their  
224 investment in indirect fitness opportunities (helping to rear non-descendent offspring).  
225 This is in line with theoretical predictions that parental manipulation of the cooperative  
226 behaviour of offspring can evolve if the costs of resisting the parental effect are high and  
227 inclusive fitness benefits of helping rear subsequent offspring are high (18).

228         Control dominant females that were fed during pregnancy produced daughters  
229 that were larger during early development (1-3 months) compared to daughters from  
230 cortisol-treated or untreated litters. Although mothers that were treated with cortisol  
231 during pregnancy received the same amount of food as controls, daughters and sons  
232 from mothers fed cortisol during pregnancy did not differ in body mass compared to

233 those from untreated litters. This indicates that the additional food provided to dominant  
234 females during pregnancy had the potential to increase growth, but the added cortisol  
235 prevented those gains in body mass. This has implications for understanding the fitness  
236 consequences of maternal stress on offspring growth trajectories (15, 43) because our  
237 results show that elevated circulating glucocorticoid levels in pregnant females in the  
238 absence of energetic constraints induced reductions in the early life growth of offspring.  
239 This supports the hypothesis that maternal stress levels during offspring development  
240 act as a cue that induces plasticity in offspring growth rather than simply mediating the  
241 effects of energetic constraints.

242         The reductions in the activity of the neuroendocrine stress axis of daughters may  
243 have potentiated the increased alloparental care behaviour that we observed.  
244 Compared to daughters from control litters, daughters from mothers treated with cortisol  
245 during pregnancy exhibited more babysitting as they became older, more overall pup  
246 feeding, and they also had lower plasma cortisol and fGCM concentrations. Males from  
247 mothers treated with cortisol during pregnancy had significantly lower plasma cortisol  
248 concentrations, but not fGCM concentrations as they got older and also tended to  
249 exhibit more babysitting as they aged. The activity of the neuroendocrine stress axis is  
250 closely linked to an array of social behaviours (44) and our recent work shows that  
251 elevated activity of the neuroendocrine stress axis reduces babysitting in both females  
252 and males and decreases pupfeeding in females (38). Together, this supports the  
253 hypothesis that the mechanism by which early life stress increases the cooperative  
254 behaviour of daughters is by dampening the activity of their neuroendocrine stress axis.

255           Our results show that the effects of maternal stress on offspring growth,  
256   physiology, and behaviour were greater in daughters than in sons, which adds to  
257   biomedical (45-46) and ecological (47-49) studies that highlight how early life conditions  
258   or maternal stress levels can have sex-specific consequences for offspring. In  
259   meerkats, there may be added benefits for the dominant female for altering the  
260   cooperative behaviour of daughters compared to sons; daughters exhibit more  
261   cooperative behaviour than sons (35) and are more responsive to the begging calls of  
262   subsequent offspring that they provision with food (50). More broadly, sex-differences in  
263   natal dispersal may cause these differential responses to parental effects. In meerkats,  
264   subordinate males voluntarily disperse from their natal group to look for receptive  
265   females but can return to their natal group whereas subordinate females rarely  
266   voluntarily disperse from their natal group (51). In our case and in others (43), the more  
267   philopatric sex (females) is more sensitive to early life conditions, which may be due to  
268   differential costs of parental modification between the philopatric and dispersing sex. If  
269   parental effects have long-term consequences on offspring characteristics, as we show  
270   here, there may be an increased degree of mismatch between the phenotype of the  
271   dispersing sex and the postnatal environment where individuals eventually settle. If this  
272   mismatch has fitness costs, this should select for individuals from the dispersing sex to  
273   be less responsive to cues from the parental phenotype or environment.

274           Our results provide some support for the hypothesis that parents may alter the  
275   cooperative tendencies of their offspring by manipulating the characteristics of their  
276   offspring (9-10). Explanations regarding the evolutionary origins of cooperative  
277   behaviour involve nepotism or kin selection (52), mutualisms or reciprocity (53), but few

278 studies have tested the “parental manipulation” hypothesis proposed by Alexander (9).  
279 Some studies show that alleles that increase maternal fitness at the expense of the  
280 direct fitness of offspring can evolve (19) and that cooperative breeders may bias  
281 investment towards offspring that exhibit more cooperative behaviour (54). Our study  
282 provides evidence that environmental stressors and parental effects can modify the  
283 cooperative tendencies of their offspring.

284 Finally, our results have two implications for theoretical models examining the  
285 evolution of parental effects. First, given the sex-specificity of parental effects, our  
286 results challenge the conclusions of models examining the evolution of parental effects  
287 that assume that all offspring are equally sensitive to the parental effect (16), or those  
288 that assume that the benefits of exhibiting the phenotype resulting from the parental  
289 effect are equal for all offspring (18). Second, selfish parental effects are thought to be  
290 relatively rare (8, 13) and theory (16-17) and empirical studies showing sex-specific  
291 responses to early life stress (45-46) indicate that offspring can become resistant to  
292 such selfish parental effects. However, the evolution of selfish parental effects may be  
293 dependent upon the social environment (24) especially if the selfish parental effect  
294 influences the expression of alloparental care behaviour of offspring and therefore  
295 increases the indirect fitness of offspring. Our results provide an example whereby a  
296 stress-mediated maternal effect reduces the direct fitness of daughters (by reducing  
297 their early life growth), but presumably increases the direct fitness of mothers and  
298 indirect fitness of daughters by elevating their cooperative behaviour.

299

300

## 301 **Methods**

### 302 *Study site*

303 We studied free-living meerkats at the Kuruman River Reserve (26° 58' S, 21°  
304 49' E) in the Northern Cape, South Africa from 2014-2017. Individuals were marked  
305 uniquely (with PIT tags: Identipet®, Johannesburg, South Africa) as well as dye marks  
306 so that they could be identified. Groups were visited for ~4-8 hours per day ~4-6 times  
307 per week throughout each year of study and sometimes more frequently such as when  
308 there were pups being babysat.

### 309 *Experimental manipulations of dominant females*

310 Dominant females in each group were identified via behavioural observations  
311 (55). During each visit, we recorded which individuals were present as well as their body  
312 mass. Meerkats were weighed on a portable balance each morning before foraging, 2-4  
313 hrs after foraging was initiated, and immediately prior to when foraging ended (56). The  
314 pregnancy status of dominant females was determined visually (distended abdomen) as  
315 well as noting a constant increase in their body mass.

316 Dominant females were treated with either a cortisol solution or a control oil  
317 vehicle when they were pregnant by feeding them food containing one of these two  
318 treatments. We initially offered experimental animals hard boiled egg with added cortisol  
319 but found that they rejected all foods that contained added cortisol with the exception of  
320 scorpions. We consequently fed experimental females with cortisol (10 mg/kg of  
321 hydrocortisone, Sigma H4126), that were dissolved in 100 µl of 100% coconut oil and  
322 injected into a dead scorpion (*Opisthophthalmus* spp.). Control females were fed a dead  
323 scorpion that was injected with 100 µl of 100% coconut oil. A previous study using the

324 same protocol showed that meerkats that were fed cortisol had significantly higher  
325 plasma cortisol and fGCM concentrations than control animals and these increases  
326 were within a biologically-relevant range (38). This indicated that our treatment causes  
327 the exogenous glucocorticoids that we feed the meerkats to enter their bloodstream and  
328 leads to sustained increases in their circulating glucocorticoid concentrations.

329 We aimed to experimentally increase the glucocorticoid concentrations of  
330 pregnant dominant females from when they were first confirmed to be pregnant (second  
331 half of gestation) until parturition. Meerkats have a ~70 d gestation period so we aimed  
332 to treat them with glucocorticoids from approximately 35-70 d during gestation. In  
333 reality, females that successfully produced a litter where pups emerged from the natal  
334 burrow were treated with cortisol for 12-36 days prior to birth (n=10 litters from 9  
335 females, mean = 23.7 d, median = 23.5 d) whereas controls were fed for 12-58 d prior  
336 to birth (n=6 litters from 6 females, mean = 30 d, median = 20.5 d).

337 Females were randomly allocated to the treatments. Across the three years of  
338 this study, we produced a total of 16 cortisol-treated or control litters produced by 12  
339 dominant females in 12 different social groups. Three of the females experienced both  
340 the control and cortisol treatments at different time points of the experiment, whereas  
341 one female experienced the control treatment once and the cortisol treatments twice.  
342 For these latter females treated twice, the order of treatments was randomly selected.  
343 We conducted these experiments over the course of three years: 13 litters from 10  
344 females in 2014 (April-December 2014, 3 litters aborted), 5 litters from 5 females in  
345 2015 (February-July 2015, 1 litter aborted), and 3 litters from 3 females in 2016 (July  
346 2016).

347 To provide an additional comparison group to investigate how our treatments (fed  
348 during pregnancy or fed cortisol during pregnancy) affected offspring survival, body  
349 mass, and cooperative behaviour, we also monitored these traits in offspring produced  
350 by dominant females that were untreated during pregnancy (n = 52 litters from 21  
351 dominant females). For our analyses of how the treatments affected offspring survival  
352 and body mass, the untreated offspring were those from litters produced by dominant  
353 females in other meerkat groups in our same study area and were born during our study  
354 (hereafter called 'untreated' litters). We assessed the contributions of offspring from  
355 mothers treated with cortisol during pregnancy to two cooperative behaviours  
356 (babysitting and pup feeding) compared to those from control litters but also to other  
357 group members from untreated litters. We did not have data from offspring from  
358 untreated litters when we assessed how our treatments affected their plasma cortisol or  
359 fGCM concentrations.

360 *Quantifying early life growth of offspring*

361 Meerkat pups typically first emerge from their natal burrow approximately 21-30 d  
362 after birth. Meerkat groups and dominant females were monitored daily around the  
363 estimated date of parturition and birth dates were estimated according to the change in  
364 the physical appearance of the dominant female, a large drop in body mass overnight,  
365 and group members exhibiting babysitting behaviour at the sleeping burrow. Burrows  
366 containing pups were monitored each day and, when pups emerged, they were uniquely  
367 marked by trimming small sections of hair before permanent PIT tags could be applied.  
368 Pups were weighed each time we visited the groups on a portable balance in the  
369 morning after group members emerged from their sleeping burrow (as above).

370 *Quantifying cooperative behaviour of offspring*

371 We measured the babysitting (controls: 195-655 d; cortisol: 184-655 d; untreated:  
372 155-655 d) and pup feeding (controls: 220-635 d; cortisol: 184-655 d; untreated: 155-  
373 626 d) contributions of offspring from cortisol-treated and control litters when they were  
374 >6 months of age until death or disappearance. We visited sleeping burrows containing  
375 pups every day in the morning and recorded the identity of the attending babysitters. As  
376 we have done previously (33, 57), we calculated relative babysitting contributions of  
377 each individual meerkat for each litter by dividing the total number of days an individual  
378 babysat a litter over the total number of days that this specific litter had a babysitter.  
379 Pup feeding behaviour for each pup produced by the dominant females in the different  
380 treatment groups was estimated using *ad libitum* sampling (34). When the social group  
381 contained pups (up to 90 d of age), we recorded all pup-feeding events, which are  
382 visually and acoustically conspicuous to observers (58). We used the probability of pup  
383 feeding occurring and corrected for variation in observation time (see below).

384 *Quantifying plasma cortisol concentrations from offspring*

385 We obtained plasma samples from offspring from cortisol-treated and control  
386 litters approximately every 3 months from first emergence from the burrow (~1 month)  
387 until ~18 months of age (controls: 20-548 d; cortisol-treated: 25-559 d). Capture and  
388 blood processing procedures are described elsewhere (59-60). We measured total  
389 plasma cortisol concentrations using a previously validated assay (Coat-a-Count,  
390 Siemens Diagnostic Products Corporation, Los Angeles, USA: validation described in  
391 59). The sensitivity of the assay was 1.9 ng/ml and cross reactivity to other hormones  
392 was 76% with prednisolone, 11.4% with 11-deoxycortisol, 2.3% with prednisone and

393 <1% with aldosterone, corticosterone, cortisone, estriol, estrone and pregnenolone.  
394 Intra-assay coefficient of was 7% (n = 20 samples). Inter-assay coefficient of variation  
395 for a low control was 8% ( $78.5 \pm 6.3$  nmols/l, n = 5 assays) and 2.8% for a high control  
396 ( $187 \pm 5.3$  ng/ml, n = 5 assays).

#### 397 *Quantifying fGCM concentrations from offspring*

398 We collected faecal samples from offspring from cortisol-treated and control  
399 litters opportunistically during behavioural observations over the course of the study  
400 (controls: 25-356 d; cortisol-treated: 32-326 d). Faecal samples were processed as  
401 described previously using a methanol extraction to remove fGCMs (61-62).  
402 Immunoreactive fGCM concentrations were determined using an enzyme immunoassay  
403 measuring cortisol metabolites with a  $5\beta$ - $3\alpha$ , $11\beta$ -diol-structure ( $11\beta$ -  
404 hydroxyetiocholanolone) already established for monitoring fGCM alterations in  
405 meerkats (62). fGCMs measured reflect average adrenal cortisol production over the  
406 previous ~24 to 48 hr period (62). Detailed assay characteristics, including full  
407 descriptions of the assay components and cross-reactivities, are found elsewhere (63)  
408 The sensitivity of the assay was 1.2 ng/g dry weight and intra-assay coefficients of  
409 variation (CV) determined by repeated measurements of high and low value quality  
410 controls were 6.9% and 7.4%, respectively, and inter-assay CV values were 11.5% and  
411 15.9% (n = 29 assays). fGCM concentrations below are expressed as ln ng/g dry faecal  
412 matter.

#### 413 *Statistical analyses*

414 We used generalized (binomial errors) or linear mixed-effects models (LMMs) to  
415 examine how our treatments affected the probability that the litter was aborted, litter size

416 and sex ratio at emergence from the burrow, and the proportion of the litter that survived  
417 to emergence from the burrow, independence (90 d of age: 29), and 6 or 12 months of  
418 age. We focused on addressing whether the cortisol-treated litters differed from our  
419 control or untreated litters. These models included a fixed effect for date of birth of the  
420 litter and random intercept terms for dominant female identity and year (as the  
421 experiments were conducted over 3 years). None of the GLMMs were overdispersed  
422 (Table S2).

423 We used a LMM to investigate how the maternal treatments affected offspring  
424 body mass from first emergence from their natal burrow (~1 month) to 3 months of age  
425 when the pups are typically foraging independently (29, 34). Morning body mass (in  
426 grams) was the response variable with the fixed effects of maternal treatment (cortisol-  
427 treated, control, or untreated), pup sex, pup age, litter size at burrow emergence, group  
428 size, group size<sup>2</sup>, total rainfall in the previous 60 days, two measures of seasonality  
429 (sine and co-sine functions of day of weight measure: see 56), and two three-way  
430 interactions between sex, treatment, age or age<sup>2</sup>. Random intercept terms for year and  
431 the identity of the individual nested in litter, nested in dominant female identity, nested in  
432 group were also included in this model. Fixed and random effects included in these  
433 models were based upon previous studies investigating meerkat body mass and growth  
434 from 1-3 months (28, 31, 56). Only individuals that survived to 90 d were included in  
435 these analyses.

436 We assessed how the treatments affected the relative babysitting and pup  
437 feeding contributions of subordinates when they were >6 months (as they rarely do  
438 alloparental care behaviour <6 months: 35) from cortisol-treated, control, and untreated

439 litters. In these generalized linear mixed-effects models (GLMM, binomial errors), we  
440 included a three-way interaction between treatment, sex, and age of the subordinate to  
441 assess if the effects of the treatments on babysitting or pup feeding varied according to  
442 the sex or age of the subordinate, as contributions to cooperative behaviour in meerkats  
443 are known to vary according to subordinate sex and age (35). To account for  
444 differences in observation time, we included a co-variate for the number of days the  
445 litter was babysat (babysitting length) and the number of days the subordinate was  
446 observed in the group during babysitting as well as the total time spent observing the  
447 group during pup feeding (observation time). We included a range of co-variables (see  
448 Tables S4-S6) that have been previously documented to affect contributions to  
449 babysitting and pup feeding, including age, foraging success, body mass, and group  
450 size (Clutton-Brock et al., 2000, 2002, 2003; Carlson et al., 2006a; Dantzer et al.,  
451 2017a). Relatedness between the subordinate and the litter being babysat was not  
452 included as it has not been shown to impact babysitting or pup feeding contributions  
453 (27, 57) and most of the litters in our entire dataset were produced by the mother or full  
454 sibling of the subordinate. Random intercept terms for year and the identity of the  
455 individual, and litter being babysat or pup fed nested within the group where the litter  
456 was being babysat or pup fed. Overdispersion was not an issue for our GLMM for  
457 babysitting as indicated by the goodness of fit test (Pearson  $\chi^2 = 147.1$ ,  $df = 154$ ,  $P =$   
458  $0.64$ , using package `aods3`: 64) but our GLMM for pup feeding was initially  
459 overdispersed (Pearson  $\chi^2 = 310$ ,  $df=165$ ,  $P < 0.0001$ ) so we included an observation  
460 level random intercept term.

461 We used two separate LMMs to assess how our manipulations affected plasma  
462 cortisol and fGCMs in offspring from cortisol-treated and control litters. Each model  
463 included fixed effects for maternal treatment, pup sex and age, time of day and year that  
464 the sample was acquired (2014 or 2015), and random intercept terms for identity of  
465 individual nested in their birth litter and group. In the model for plasma cortisol  
466 concentrations, we also included a linear and second order fixed effect for the time it  
467 took to acquire the blood sample to control for any variation in plasma cortisol  
468 concentrations due to restraint stress (60). Year was included as a fixed effect here  
469 because we only had samples from two separate years. We included covariates  
470 associated with the individual meerkat and weather or social group characteristics that  
471 are known to affect plasma cortisol (60) or fGCM (62) concentrations (see Tables S6-  
472 S7).

473 We used R (version 3.4.3: 65) for all of our statistical analyses. R package lme4  
474 (version 1.1-14: 66) was used for LMMs and P values were estimated using lmerTest  
475 (version 2.0-33: 67). A graphical approach was used to confirm normality and  
476 homoscedasticity of residuals and to confirm there were no observations with high  
477 leverage (68). All continuous variables were standardized to a mean of 0 and SD of 1.

478  
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495 Duncan coordinated and collected data, B.D. conducted analyses and produced figures,  
496 B.D. and T.H.C-B authored manuscript with contributions from all authors.

497

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500

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509

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697 **Figure Legends**

698

699 **Figure 1.** (A) Daughters but not (B) sons from mothers treated with cortisol during  
700 pregnancy were significantly smaller from initial emergence from their natal burrow to  
701 nutritional independence (~1-3 months) compared to those from control litters  
702 (daughters: age  $\times$  treatment,  $t = -4.17$ ,  $P < 0.0001$ ; sons:  $t = -1.48$ ,  $P = 0.14$ ), but not  
703 untreated litters (daughters: age  $\times$  treatment,  $t = 0.65$ ,  $P = 0.51$ ; sons:  $t = -0.52$ ,  $P = 0.6$ ,  
704 Table S3). Data are body mass measures from offspring from cortisol-treated (females:  
705  $n = 373$  estimates; males:  $n = 488$ ), control (females:  $n = 215$ ; males:  $n = 241$ ), and  
706 untreated litters (females:  $n = 1121$ ; males:  $n = 2238$ ). Raw data and regression lines  
707 are shown (full results in Table S3).

708

709 **Figure 2.** Babysitting contributions of (A) daughters and (B) sons from mothers treated  
710 with cortisol during pregnancy increased with age at a faster rate than those from  
711 control (females:  $z = -2.89$ ,  $P = 0.0039$ ; males:  $z = -1.92$ ,  $P = 0.055$ ), but not untreated  
712 (“None”) litters (females:  $z = 1.88$ ,  $P = 0.06$ ; males:  $z = -0.03$ ,  $P = 0.97$ , Table S4). Data  
713 are relative babysitting contributions from offspring from cortisol-treated (females:  $n = 15$   
714 estimates; males:  $n = 24$ ), control (females:  $n = 15$ ; males:  $n = 10$ ), and untreated litters  
715 (females:  $n = 49$ ; males:  $n = 69$ ). Raw data and regression lines are shown (full results  
716 in Table S4).

717

718 **Figure 3.** Pup feeding contributions of (A) daughters, but not (B) sons, from mothers  
719 treated with cortisol during pregnancy were significantly higher compared to from control

720 (females:  $z = -3.09$ ,  $P = 0.0004$ ; males:  $z = -1.15$ ,  $P = 0.25$ ) or untreated (“None”) litters  
721 (females:  $z = -3.47$ ,  $P = 0.0005$ ; males:  $z = -0.89$ ,  $P = 0.37$ , Table S5). Data are relative  
722 pup feeding contributions from offspring from cortisol-treated (females:  $n = 16$   
723 estimates; males:  $n = 26$ ), control (females:  $n = 16$ ; males:  $n = 10$ ), and untreated litters  
724 (females:  $n = 64$ ; males:  $n = 71$ ). Raw data are shown (full results in Table S5). Boxplots  
725 show median (solid horizontal line), mean (grey diamonds), and first (25%) and third  
726 (75%) quartiles.

727  
728 **Figure 4.** (A) Daughters and (B) sons from mothers treated with cortisol during  
729 pregnancy had lower plasma cortisol concentrations as they became older compared to  
730 those from control litters, though the difference was only significant in males (daughters:  
731 age x treatment,  $t = -1.61$ ,  $P = 0.11$ ; sons: age x treatment  $t = -2.59$ ,  $P = 0.01$ , Table  
732 S6). Data are residual plasma cortisol concentrations from offspring from cortisol-  
733 treated (females:  $n = 64$  samples; males:  $n = 92$ ) and control (females:  $n = 89$ ; males:  $n$   
734  $= 104$ ) litters. Residuals from a linear mixed-effects model (Table S6) are shown on y-  
735 axis.

736  
737 **Figure 5.** Faecal glucocorticoid metabolite (fGCM) concentrations in (A) daughters but  
738 not (B) sons from mothers treated with cortisol during pregnancy were significantly  
739 lower than those from control litters as they became older (daughters: age x treatment,  $t$   
740  $= -2.95$ ,  $P = 0.0033$ ; sons: age x treatment,  $t = -0.49$ ,  $P = 0.62$ , Table S7. Data are  
741 residual fGCM concentrations from offspring from cortisol-treated (females:  $n = 79$

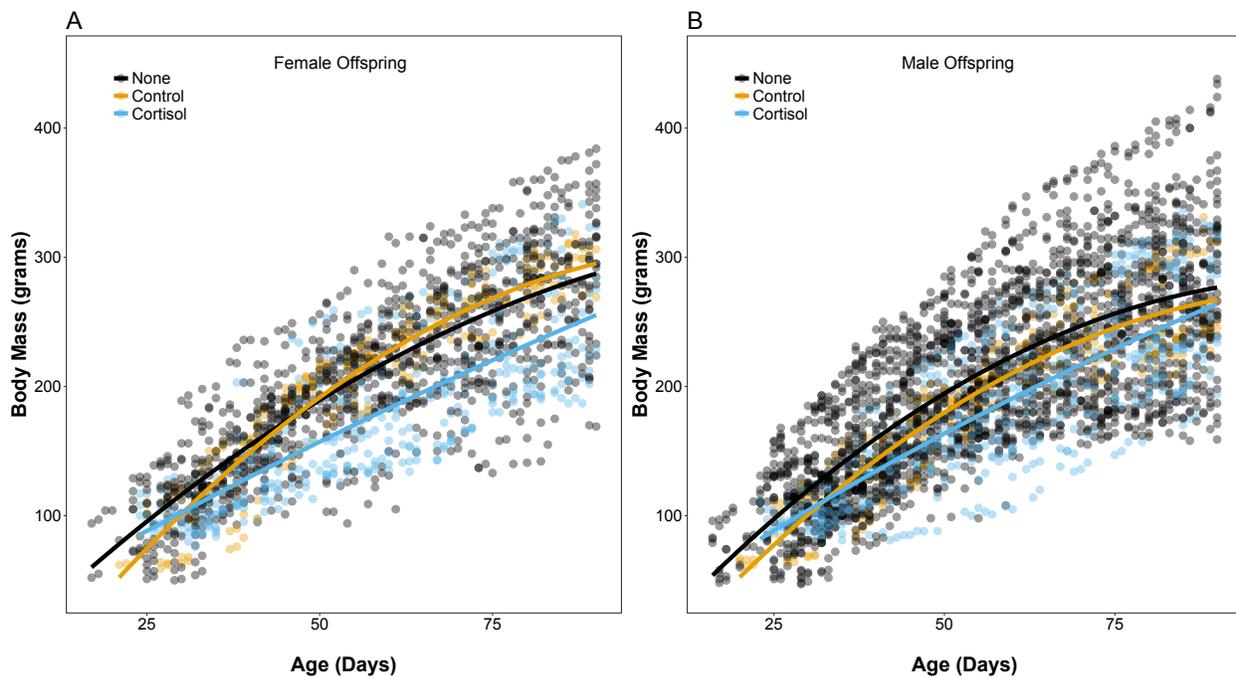
742 samples; males: n = 118) and control (females: n = 154; males: n = 201) litters.

743 Residuals from a linear mixed-effects model (Table S7) are shown on y-axis.

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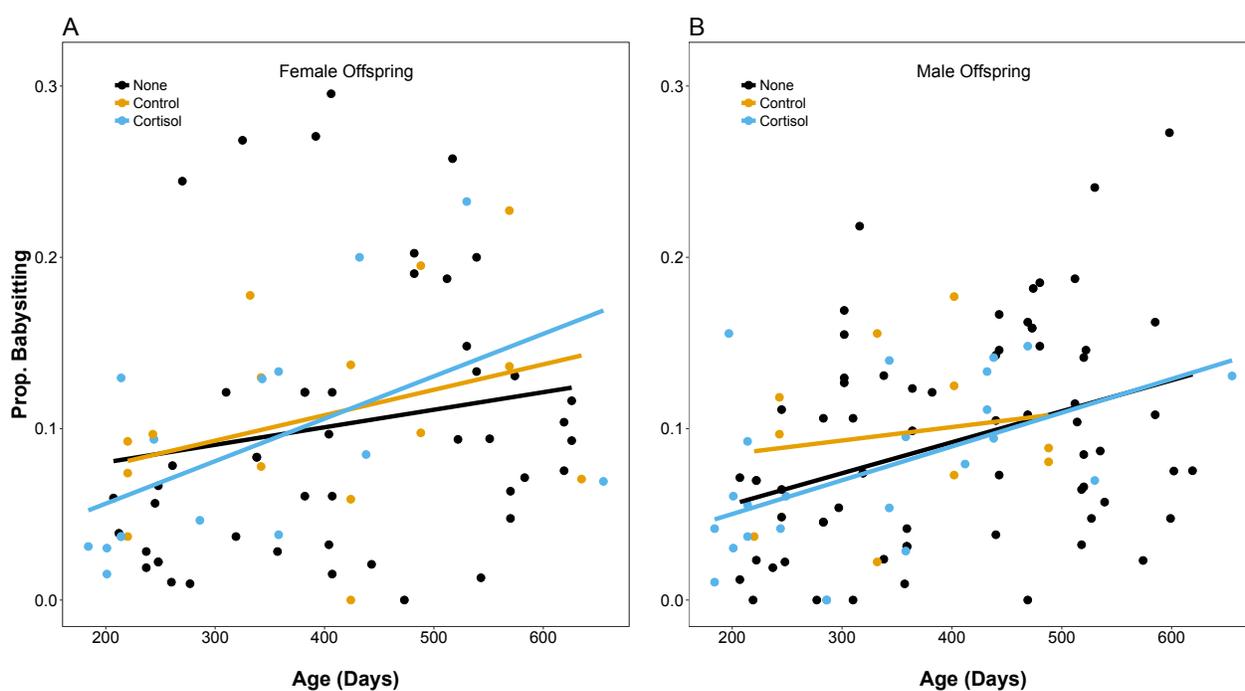
746 **Figure 1.** (A) Daughters but not (B) sons from mothers treated with cortisol during  
747 pregnancy were significantly smaller from initial emergence from their natal burrow to  
748 nutritional independence (~1-3 months) compared to those from control litters  
749 (daughters: age  $\times$  treatment,  $t = -4.17$ ,  $P < 0.0001$ ; sons:  $t = -1.48$ ,  $P = 0.14$ ), but not  
750 untreated litters (daughters: age  $\times$  treatment,  $t = 0.65$ ,  $P = 0.51$ ; sons:  $t = -0.52$ ,  $P = 0.6$ ,  
751 Table S3). Data are body mass measures from offspring from cortisol-treated (females:  
752  $n = 373$  estimates; males:  $n = 488$ ), control (females:  $n = 215$ ; males:  $n = 241$ ), and  
753 untreated litters (females:  $n = 1121$ ; males:  $n = 2238$ ). Raw data and regression lines  
754 are shown (full results in Table S3).



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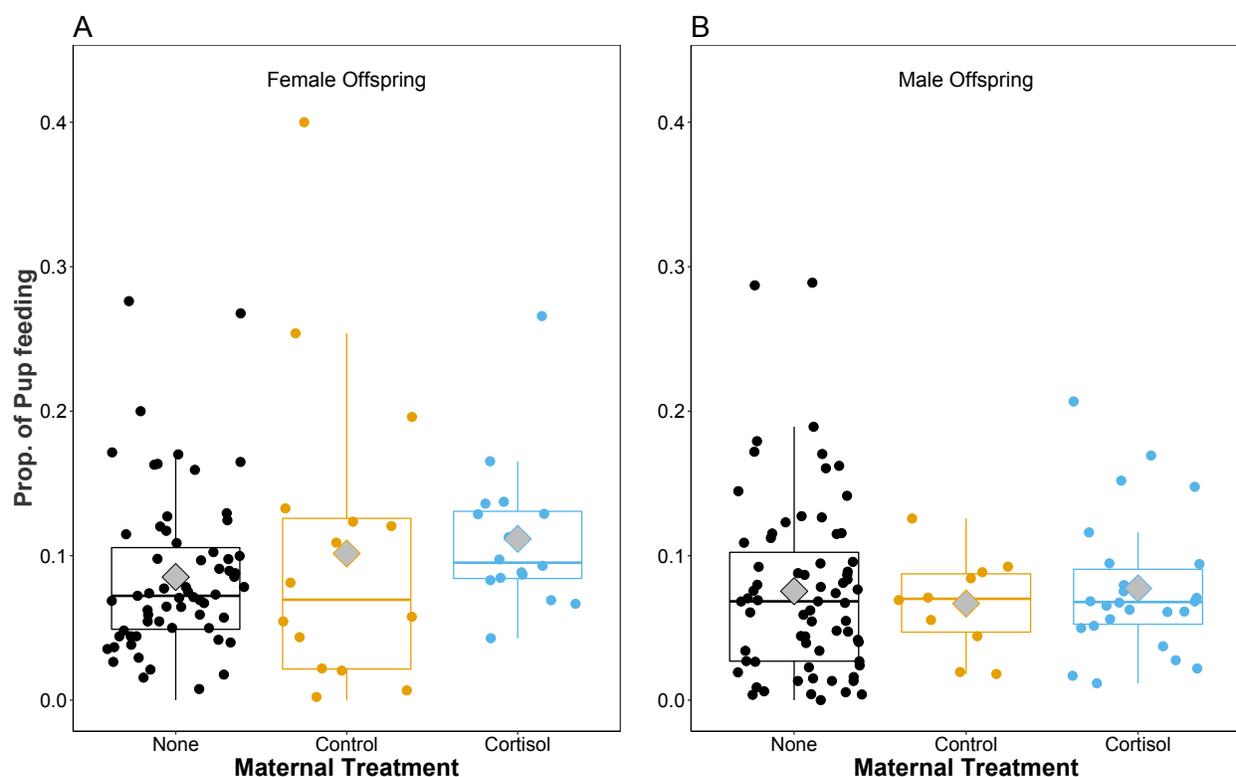
757 **Figure 2.** Babysitting contributions of (A) daughters and (B) sons from mothers treated  
758 with cortisol during pregnancy increased with age at a faster rate than those from  
759 control (females:  $z = -2.89$ ,  $P = 0.0039$ ; males:  $z = -1.92$ ,  $P = 0.055$ ), but not untreated  
760 (“None”) litters (females:  $z = 1.88$ ,  $P = 0.06$ ; males:  $z = -0.03$ ,  $P = 0.97$ , Table S4). Data  
761 are relative babysitting contributions from offspring from cortisol-treated (females:  $n = 15$   
762 estimates; males:  $n = 24$ ), control (females:  $n = 15$ ; males:  $n = 10$ ), and untreated litters  
763 (females:  $n = 49$ ; males:  $n = 69$ ). Raw data and regression lines are shown (full results  
764 in Table S4).



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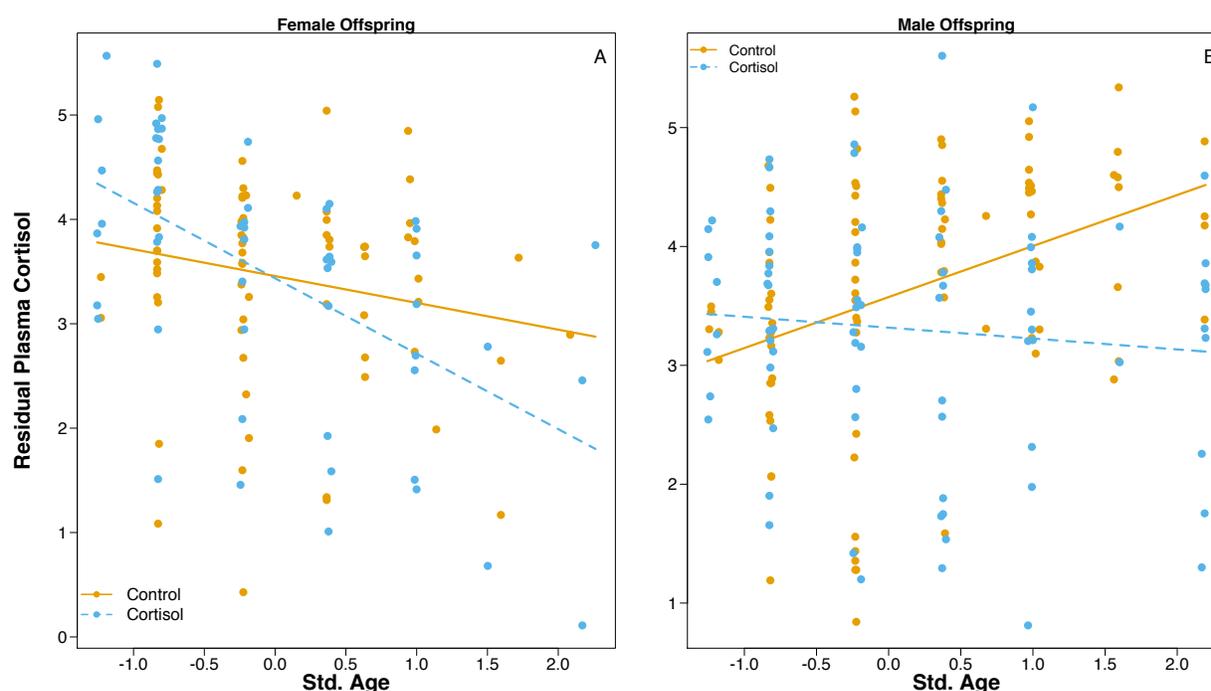
767 **Figure 3.** Pup feeding contributions of (A) daughters, but not (B) sons, from mothers  
768 treated with cortisol during pregnancy were significantly higher compared to from control  
769 (females:  $z = -3.09$ ,  $P = 0.0004$ ; males:  $z = -1.15$ ,  $P = 0.25$ ) or untreated (“None”) litters  
770 (females:  $z = -3.47$ ,  $P = 0.0005$ ; males:  $z = -0.89$ ,  $P = 0.37$ , Table S5). Data are relative  
771 pup feeding contributions from offspring from cortisol-treated (females:  $n = 16$   
772 estimates; males:  $n = 26$ ), control (females:  $n = 16$ ; males:  $n = 10$ ), and untreated litters  
773 (females:  $n = 64$ ; males:  $n = 71$ ). Raw data are shown (full results in Table S5). Boxplots  
774 show median (solid horizontal line), mean (grey diamonds), and first (25%) and third  
775 (75%) quartiles.



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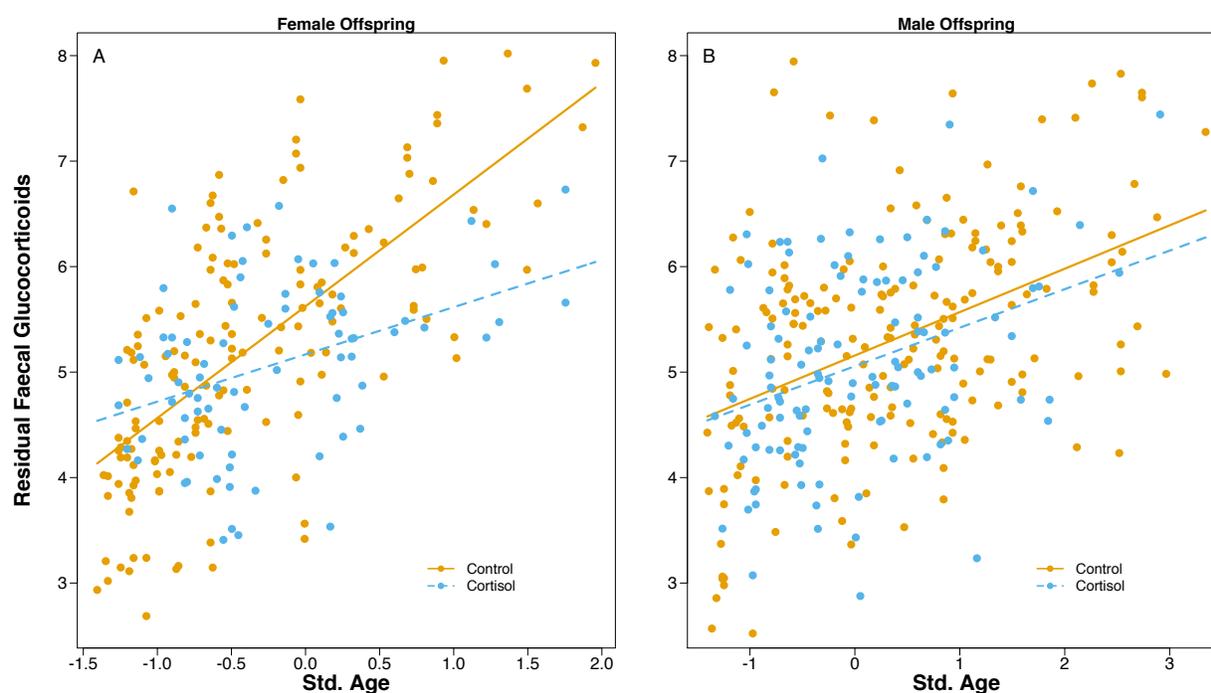
778 **Figure 4.** (A) Daughters and (B) sons from mothers treated with cortisol during  
779 pregnancy had lower plasma cortisol concentrations as they became older compared to  
780 those from control litters, though the difference was only significant in males (daughters:  
781 age x treatment,  $t = -1.61$ ,  $P = 0.11$ ; sons: age x treatment  $t = -2.59$ ,  $P = 0.01$ , Table  
782 S6). Data are residual plasma cortisol concentrations from offspring from cortisol-  
783 treated (females:  $n = 64$  samples; males:  $n = 92$ ) and control (females:  $n = 89$ ; males:  $n$   
784  $= 104$ ) litters. Residuals from a linear mixed-effects model (Table S6) are shown on y-  
785 axis.



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788 **Figure 5.** Faecal glucocorticoid metabolite (fGCM) concentrations in (A) daughters but  
789 not (B) sons from mothers treated with cortisol during pregnancy were significantly  
790 lower than those from control litters as they became older (daughters: age x treatment,  $t$   
791 = -2.95,  $P = 0.0033$ ; sons: age x treatment,  $t = -0.49$ ,  $P = 0.62$ , Table S7. Data are  
792 residual fGCM concentrations from offspring from cortisol-treated (females:  $n = 79$   
793 samples; males:  $n = 118$ ) and control (females:  $n = 154$ ; males:  $n = 201$ ) litters.  
794 Residuals from a linear mixed-effects model (Table S7) are shown on y-axis.



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*ESM for Maternal stress increases cooperative behaviour of offspring in wild meerkats by Dantzer et al.*

**Electronic Supplementary Material**

***Maternal stress increases cooperative behaviour of offspring in wild meerkats***

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Tables S1-S7

*ESM for Maternal stress increases cooperative behaviour of offspring in wild meerkats by Dantzer et al.*

**Table S1. Sample sizes and effects of dominant female treatments on litter characteristics and offspring survival.** Means and standard deviations are shown. The number of litters aborted for untreated females was not known. Number of pups emerged correspond to those that emerged from the natal burrow. Three cortisol-treated litters and 1 control litter were aborted prior to birth and are not shown below. Litter sex ratio is the proportion of males in the litter. In some of the untreated litters, sex of the pups was not known (they died before sexing) and so are listed as unknown (“Unk”).

<b>Treatment</b>	<b>Total # litters &amp; females treated</b>	<b>Total # pups emerged (F, M, Unk)</b>	<b>Avg. Pups emerged</b>	<b>Avg. Pups Surviving to 3 months</b>	<b>Avg. Pups Surviving to 6 months</b>	<b>Avg. Pups Surviving to 12 months</b>
Untreated	52 (21 females)	49 F, 84 M, 52 Unk	3.78 ± 1.23	2.68 ± 1.58	2.1 ± 1.63	1.62 ± 1.54
Control	7 (6 females)	12 F, 13 M	4.17 ± 0.98	3.83 ± 1.17	3.83 ± 1.17	2.83 ± 1.94
Cortisol	13 (10 females)	13 F, 18 M	3.87 ± 0.83	3.25 ± 1.03	2.75 ± 1.28	1.75 ± 1.75

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**Table S2. Effects of dominant female treatments on litter characteristics and pup survival.** Results are from a linear mixed-effects model (# pups emerged) or generalized linear mixed-effects models (GLMMs, all other response variables) that each contained random intercept terms for dominant female identity and year. No GLMM was overdispersed as indicated by goodness of fit tests (R package aods3, P-values from Pearson  $\chi^2$  tests ranged from 0.13 to 1).

Response variable	Fixed effect	b	SE	t or z	P-value
<b># Litters aborted</b>	Intercept	-1.21	0.66	-1.83	0.07
	Birthdate	-0.17	0.59	-0.29	0.77
	Treatment				
	<i>Control</i>	-0.59	1.27	-0.46	0.64
<b># Pups emerged</b>	<b>Intercept</b>	<b>3.9</b>	<b>0.42</b>	<b>9.36</b>	<b>&lt;0.0001</b>
	Birthdate	0.02	0.16	0.11	0.91
	Treatment				
	<i>Control</i>	0.3	0.62	0.49	0.63
	<i>Untreated</i>	-0.11	0.45	-0.25	0.8
<b>Litter sex ratio</b>	Intercept	-0.54	0.3	-1.84	0.066
	Birthdate	0.02	0.12	0.15	0.88
	Treatment				
	<i>Control</i>	-0.11	0.45	-0.23	0.81
	<i>Untreated</i>	0.09	0.33	0.27	0.78
<b>Prop. litter surviving to 3 months</b>	Intercept	-0.16	0.27	-0.62	0.53
	Birthdate	-0.12	0.11	-1.09	0.27
	Treatment				
	<i>Control</i>	0.06	0.39	0.16	0.87
	<i>Untreated</i>	-0.19	0.3	-0.64	0.52
<b>Prop. litter surviving to 6 months</b>	Intercept	-0.32	0.28	-1.16	0.24
	Birthdate	-0.19	0.11	-1.65	0.099
	Treatment				
	<i>Control</i>	0.21	0.4	0.52	0.6
	<i>Untreated</i>	-0.28	0.31	-0.91	0.36
<b>Prop. litter surviving to 12 months</b>	<b>Intercept</b>	<b>-0.91</b>	<b>0.46</b>	<b>-1.999</b>	<b>0.046</b>
	Birthdate	-0.22	0.14	-1.58	0.11
	Treatment				
	<i>Control</i>	0.36	0.46	0.79	0.43
	<i>Untreated</i>	0.096	0.38	0.25	0.8

Reference for Treatment was cortisol-treated litters. Data other than # litters aborted are based upon an initial sample size of offspring from untreated (195 pups from 52 litters produced by 21 dominant females), control (25 pups from 6 litters produced by 6 females), or cortisol-treated (31 pups from 10 litters produced by 9 females) litters that produced pups that emerged from the burrow.

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**Table S3. Effect of dominant female treatments on offspring body mass from emergence to nutritional independence (1-3 months of age).** Data are from a linear mixed-effects model where the response variable was morning body mass that contained random intercept terms for individual identity nested in birth litter nested in mother nested in natal group ( $\sigma^2 = 116.7$ ) and year ( $\sigma^2 = 0$ ).

<b>Fixed Effect</b>	<b>b</b>	<b>SE</b>	<b>t</b>	<b>df</b>	<b>P-value</b>
<b>Intercept</b>					
<i>Females</i>	<b>184.6</b>	<b>9.75</b>	<b>18.93</b>	<b>53</b>	<b>&lt;0.0001</b>
<i>Males</i>	<b>189.1</b>	<b>9.5</b>	<b>19.8</b>	<b>49</b>	<b>&lt;0.0001</b>
Litter size	-5.31	3.9	-1.37	48	0.18
<b>First weight</b>	<b>15.96</b>	<b>2.52</b>	<b>6.344</b>	<b>166</b>	<b>&lt;0.0001</b>
Sex (M)	4.54	4.32	1.05	171	0.29
<b>Age</b>	<b>53.3</b>	<b>1.06</b>	<b>50.4</b>	<b>4569</b>	<b>&lt;0.0001</b>
<b>Age<sup>2</sup></b>	<b>-4.76</b>	<b>1.15</b>	<b>-4.12</b>	<b>4516</b>	<b>&lt;0.0001</b>
<b>Rainfall</b>	<b>2.81</b>	<b>0.61</b>	<b>4.57</b>	<b>4550</b>	<b>&lt;0.0001</b>
<b>Season (Sine)</b>	<b>-67.2</b>	<b>3.3</b>	<b>-20.6</b>	<b>4238</b>	<b>&lt;0.0001</b>
<b>Season (Co-sine)</b>	<b>66.22</b>	<b>3.4</b>	<b>19.2</b>	<b>4191</b>	<b>&lt;0.0001</b>
Group size	2.3	2.66	0.86	109	0.39
Group size <sup>2</sup>	-0.09	2.21	-0.04	178	0.97
Treatment (Control)					
<i>Females</i>	22.6	15.6	1.45	52	0.15
<i>Males</i>	12.9	15.5	0.83	50	0.41
<b>Treatment (None)</b>					
<i>Females</i>	<b>23.6</b>	<b>10.6</b>	<b>2.23</b>	<b>54</b>	<b>0.029</b>
<i>Males</i>	<b>22.9</b>	<b>10.4</b>	<b>2.22</b>	<b>50</b>	<b>0.031</b>
Age x Sex (M)	1.64	1.37	1.19	4567	0.23
Age <sup>2</sup> x Sex (M)	1.02	1.53	0.67	4543	0.5
Sex (M) x Treatment (Control)	-9.73	7.7	-1.27	164	0.21
Sex (M) x Treatment (None)	-0.63	5.1	-0.12	172	0.9
<b>Age x Treatment (Control)</b>					
<i>Females</i>	<b>7.6</b>	<b>1.8</b>	<b>4.17</b>	<b>4595</b>	<b>&lt;0.0001</b>
<i>Males</i>	-2.3	1.5	-1.48	4548	0.14
Age x Treatment (None)					
<i>Females</i>	0.79	1.2	0.65	4574	0.51
<i>Males</i>	-0.53	1.01	-0.52	4580	0.6
Age <sup>2</sup> x Treatment (Control)					
<i>Females</i>	-0.13	1.93	-0.07	4521	0.94
<i>Males</i>	-1.05	1.6	-0.65	4547	0.52
<b>Age<sup>2</sup> x Treatment (None)</b>					
<i>Females</i>	-2.6	1.3	-1.96	4534	0.051
<i>Males</i>	<b>-6.9</b>	<b>1.1</b>	<b>-6.23</b>	<b>4556</b>	<b>&lt;0.0001</b>
<b>Age x Treatment (Control) x Sex (M)</b>	<b>-9.9</b>	<b>2.3</b>	<b>-4.23</b>	<b>4574</b>	<b>&lt;0.0001</b>
Age x Treatment (None) x Sex (M)	-1.3	1.6	-0.84	4581	0.4
Age <sup>2</sup> x Treatment (Control) x Sex (M)	-0.93	2.5	-0.37	4552	0.71
<b>Age<sup>2</sup> x Treatment (None) x Sex (M)</b>	<b>-4.3</b>	<b>1.7</b>	<b>-2.5</b>	<b>4552</b>	<b>0.01</b>

Data used in these analyses were 4676 measures of body mass from 195 meerkats produced by 21 dominant females across 53 different litters in 16 different social groups in three different years. Only offspring that survived to 90 days of age were included in these analyses.

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**Table S4. Effect of dominant female treatments on relative babysitting contributions.** Data are from a generalized linear mixed-effects model where the response variable is the proportion of babysitting exhibited by the subordinate meerkat relative to the total babysitting contributions the litter received. The model contained random intercept terms for individual ( $\sigma^2 = 0.12$ ), litter nested within group ( $\sigma^2 = < 0.0001$ ), and year ( $\sigma^2 = 0.000$ ).

<b>Fixed Effect</b>	<b>b</b>	<b>SE</b>	<b>z</b>	<b>P-value</b>
<b>Intercept</b>				
<i>Females</i>	<b>-2.1</b>	<b>0.22</b>	<b>-9.37</b>	<b>&lt; 0.0001</b>
<i>Males</i>	<b>-2.14</b>	<b>0.19</b>	<b>-11.01</b>	<b>&lt; 0.0001</b>
<b>Babysitting length</b>	<b>0.24</b>	<b>0.08</b>	<b>2.77</b>	<b>0.0056</b>
<b>Observation time</b>	<b>-0.28</b>	<b>0.08</b>	<b>-3.4</b>	<b>0.0007</b>
Litter size	0.015	0.05	0.32	0.75
Mixed Litter?	-0.04	0.12	-0.31	0.76
Sex (M)	-0.03	0.27	-0.13	0.9
<b>Age</b>				
<i>Females</i>	0.13	0.17	0.75	0.45
<i>Males</i>	<b>0.4</b>	<b>0.19</b>	<b>2.77</b>	<b>0.0056</b>
Foraging success	-0.05	0.05	-0.99	0.32
<b>Mass</b>				
<i>Females</i>	<b>-0.32</b>	<b>0.12</b>	<b>-2.61</b>	<b>0.009</b>
<i>Males</i>	-0.098	0.14	-0.7	0.48
<b>Group size</b>				
<i>Females</i>	<b>-0.35</b>	<b>0.09</b>	<b>-3.97</b>	<b>&lt; 0.0001</b>
<i>Males</i>	<b>-0.27</b>	<b>0.08</b>	<b>-3.28</b>	<b>0.001</b>
<b>Treatment (Control)</b>				
<i>Females</i>	<b>-0.67</b>	<b>0.31</b>	<b>-2.14</b>	<b>0.032</b>
<i>Males</i>	-0.12	0.28	-0.43	0.67
Treatment (None)				
<i>Females</i>	-0.06	0.23	-0.25	0.8
<i>Males</i>	-0.16	0.18	-0.85	0.39
Foraging success x Mass	0.036	0.06	0.57	0.57
<b>Age x Mass</b>				
<i>Females</i>	<b>-0.47</b>	<b>0.09</b>	<b>-5.08</b>	<b>&lt; 0.0001</b>
<i>Males</i>	<b>-0.29</b>	<b>0.08</b>	<b>-3.79</b>	<b>0.0001</b>
Age x Sex (M)	0.28	0.23	1.18	0.24
Mass x Sex (M)	0.22	0.17	1.26	0.21
Group size x Sex (M)	0.07	0.1	0.77	0.44
Treatment (Control) x Sex (M)	0.55	0.42	1.31	0.19
Treatment (None) x Sex (M)	-0.1	0.28	-0.36	0.72
<b>Age x Treatment (Control)</b>				
<i>Females</i>	<b>-0.62</b>	<b>0.21</b>	<b>-2.89</b>	<b>0.0039</b>
<i>Males</i>	-0.52	0.27	-1.92	0.055
Age x Treatment (None)				
<i>Females</i>	0.34	0.18	1.88	0.059
<i>Males</i>	-0.006	0.16	-0.03	0.97
Age x Mass x Sex	0.18	0.12	1.5	0.13
Age x Treatment (Control) x Sex (M)	0.09	0.34	0.28	0.78
Age x Treatment (None) x Sex (M)	-0.34	0.24	-1.45	0.14

Data used in these analyses were 182 observations of relative babysitting contributions to 28 litters produced in 9 groups across 3 years recorded from 105 subordinate meerkats.

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**Table S5. Effect of dominant female treatments on relative pup feeding contributions.** Data are from a generalized linear mixed-effects model where the response variable is the proportion of pup feeds exhibited by the subordinate meerkat relative to the total pup feeds the litter received. The model contained random intercept terms for individual ( $\sigma^2 = 0.000$ ), litter nested within group ( $\sigma^2 = 0.2$ ), year ( $\sigma^2 = 0.08$ ), and an observational level random intercept term to control for overdispersion ( $\sigma^2 = 0.19$ ).

<b>Fixed Effect</b>	<b>b</b>	<b>SE</b>	<b>z</b>	<b>P-value</b>
<b>Intercept</b>				
<i>Females</i>	<b>-2.27</b>	<b>0.28</b>	<b>-8.2</b>	<b>&lt;0.0001</b>
<i>Males</i>	<b>-2.66</b>	<b>0.25</b>	<b>-10.45</b>	<b>&lt;0.0001</b>
<b>Observation time</b>	<b>0.59</b>	<b>0.06</b>	<b>9.41</b>	<b>&lt;0.0001</b>
Litter size	-0.055	0.1	-0.55	0.58
Mixed litter (Y)	-0.03	0.29	-0.1	0.92
Sex (M)	-0.39	0.2	-1.93	0.053
<b>Age</b>				
<i>Females</i>	<b>-0.37</b>	<b>0.16</b>	<b>-2.33</b>	<b>0.019</b>
<i>Males</i>	<b>0.29</b>	<b>0.14</b>	<b>2.07</b>	<b>0.039</b>
<b>Foraging success</b>	<b>0.14</b>	<b>0.06</b>	<b>2.12</b>	<b>0.033</b>
<b>Mass</b>				
<i>Females</i>	0.1	0.11	0.91	0.36
<i>Males</i>	<b>-0.37</b>	<b>0.11</b>	<b>-3.4</b>	<b>0.0007</b>
<b>Group size</b>				
<i>Females</i>	<b>-0.48</b>	<b>0.13</b>	<b>-3.57</b>	<b>0.0003</b>
<i>Males</i>	<b>-0.32</b>	<b>0.13</b>	<b>-2.46</b>	<b>0.014</b>
<b>Treatment (Control)</b>				
<i>Females</i>	<b>-0.73</b>	<b>0.23</b>	<b>-3.12</b>	<b>0.0018</b>
<i>Males</i>	-0.24	0.21	-1.14	0.25
<b>Treatment (None)</b>				
<i>Females</i>	<b>-0.64</b>	<b>0.18</b>	<b>-3.49</b>	<b>0.0005</b>
<i>Males</i>	-0.14	0.13	-1.03	0.3
Foraging success x Mass	0.06	0.06	0.97	0.33
<b>Age x Mass</b>				
<i>Females</i>	-0.04	0.07	-0.62	0.54
<i>Males</i>	<b>-0.19</b>	<b>0.07</b>	<b>-2.68</b>	<b>0.007</b>
<b>Age x Sex (M)</b>	<b>0.66</b>	<b>0.19</b>	<b>3.49</b>	<b>0.00048</b>
<b>Mass x Sex (M)</b>	<b>-0.47</b>	<b>0.13</b>	<b>-3.63</b>	<b>0.0003</b>
Group size x Sex (M)	0.16	0.08	1.89	0.059
Treatment (Control) x Sex (M)	0.49	0.31	1.58	0.11
<b>Treatment (None) x Sex (M)</b>	<b>0.5</b>	<b>0.22</b>	<b>2.23</b>	<b>0.023</b>
<b>Age x Treatment (Control)</b>				
<i>Females</i>	-0.11	0.22	-0.5	0.61
<i>Males</i>	0.03	0.29	0.11	0.91
<b>Age x Treatment (None)</b>				
<i>Females</i>	0.17	0.16	1.03	0.3
<i>Males</i>	-0.02	0.14	-0.12	0.9
Age x Mass x Sex	-0.14	0.09	-1.51	0.13
Age x Treatment (Control) x Sex (M)	0.14	0.34	0.42	0.67
Age x Treatment (None) x Sex (M)	-0.19	0.21	-0.91	0.36

Data used in these analyses were 192 observations of relative pup feeding contributions to 26 litters produced in 7 groups across 3 years recorded from 101 subordinate meerkats.

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**Table S6. Effect of dominant female treatments on plasma cortisol concentrations.** Data are from a linear mixed-effects model where the response variable is plasma cortisol concentrations (ln transformed) of the subordinate meerkat. The model contained random intercept terms for individual nested within their birth litter ( $\sigma^2 = 0.042$ ), and capture group ( $\sigma^2 = 0.000$ ).

<b>Fixed Effect</b>	<b>b</b>	<b>SE</b>	<b>t</b>	<b>df</b>	<b>P-value</b>
<b>Intercept</b>					
<i>Females</i>	<b>3.18</b>	<b>0.29</b>	<b>11.14</b>	<b>120</b>	<b>&lt;0.0001</b>
<i>Males</i>	<b>3.32</b>	<b>0.26</b>	<b>12.68</b>	<b>111</b>	<b>&lt;0.0001</b>
<b>Sampling time</b>	<b>1.15</b>	<b>0.10</b>	<b>11.74</b>	<b>260</b>	<b>&lt;0.0001</b>
<b>Sampling time<sup>2</sup></b>	<b>-0.24</b>	<b>0.03</b>	<b>-7.27</b>	<b>267</b>	<b>&lt;0.0001</b>
Time of day	-0.2	0.14	-1.37	275	0.17
Sample year (2015)	0.46	0.24	1.89	220	0.06
Sex (M)	0.19	0.2	0.91	37	0.37
Age					
<i>Females</i>	-0.1	0.24	-0.41	266	0.68
<i>Males</i>	0.12	0.21	0.57	250	0.57
Body mass	-0.19	0.21	0.89	230	0.37
Foraging success					
<i>Females</i>	-0.1	0.12	-0.84	226	0.4
<i>Males</i>	-0.11	0.11	-0.96	262	0.34
Group size	0.055	0.11	0.49	240	0.62
Group size <sup>2</sup>	0.048	0.08	0.58	211	0.56
Pups in group	-0.28	0.18	-1.53	275	0.12
<b>Group sex ratio</b>	<b>0.19</b>	<b>0.08</b>	<b>2.35</b>	<b>183</b>	<b>0.02</b>
Relatedness	-0.1	0.18	-0.57	41	0.57
Weather (PC1)	-0.1	0.11	-0.94	275	0.35
Treatment (Cortisol)					
<i>Females</i>	-0.03	0.25	-0.11	39	0.91
<i>Males</i>	-0.31	0.19	-1.59	33	0.12
Sex (M) x Age	0.22	0.22	1	272	0.32
Sex (M) x Foraging success	-0.01	0.14	-0.07	257	0.94
Sex (M) x Treatment (Cortisol)	-0.29	0.3	-0.93	34	0.36
<b>Age x Treatment (Cortisol)</b>					
<i>Females</i>	-0.39	0.24	-1.61	275	0.11
<i>Males</i>	<b>-0.49</b>	<b>0.19</b>	<b>-2.59</b>	<b>274</b>	<b>0.01</b>
Group size x Pups Present (Yes)	-0.05	0.15	-0.37	215	0.71
Group size <sup>2</sup> x Pups Present (Yes)	0.07	0.12	0.55	264	0.58
Group size x Weather (PC1)	-0.04	0.08	-0.49	273	0.62
Age x Sex (M) x Treatment (Cortisol)	-0.097	0.31	-0.31	274	0.75

Data used in these analyses were 299 measures of plasma cortisol concentrations from 49 subordinate meerkats produced in 14 litters from 10 different groups. Reference levels (intercept) for “Sex” was female, “Pups in group” was Yes, and for Relatedness was “No parent was dominant”.

*ESM for Maternal stress increases cooperative behaviour of offspring in wild meerkats by Dantzer et al.*

**Table S7. Effect of dominant female treatments on faecal glucocorticoid metabolite (fGCM) concentrations.** Data are from a linear mixed-effects model where the response variable fGCM concentrations (ln+1 transformed) of the subordinate meerkat. The model contained random intercept terms for individual nested within their birth litter ( $\sigma^2 = 0.10$ ) and collection group ( $\sigma^2 = 0.000$ ).

<b>Fixed Effect</b>	<b>b</b>	<b>SE</b>	<b>t</b>	<b>df</b>	<b>P-value</b>
<b>Intercept</b>					
<i>Females</i>	<b>5.49</b>	<b>0.27</b>	<b>20.1</b>	<b>32</b>	<b>&lt;0.0001</b>
<i>Males</i>	<b>5.4</b>	<b>0.25</b>	<b>21.6</b>	<b>18</b>	<b>&lt;0.0001</b>
<b>Time of day</b>	<b>-0.14</b>	<b>0.04</b>	<b>3.27</b>	<b>514</b>	<b>0.001</b>
Sample year (2015)	0.02	0.18	0.13	142	0.89
Sex (M)	-0.9	0.21	-0.44	21	0.67
<b>Age</b>					
<i>Females</i>	<b>0.81</b>	<b>0.27</b>	<b>3.03</b>	<b>167</b>	<b>0.0029</b>
<i>Males</i>	0.33	0.2	1.68	131	0.096
Body mass	-0.3	0.19	-1.5	317	0.13
Foraging success					
<i>Females</i>	0.21	0.13	1.57	394	0.12
<i>Males</i>	0.06	0.06	1.13	518	0.26
<b>Group size</b>	<b>0.37</b>	<b>0.12</b>	<b>3.04</b>	<b>113</b>	<b>0.003</b>
Group size2	-0.04	0.11	-0.37	462	0.71
Pups in group	-0.14	0.17	-0.84	325	0.4
<b>Group sex ratio</b>	<b>0.15</b>	<b>0.07</b>	<b>2.03</b>	<b>190</b>	<b>0.04</b>
Relatedness	0.18	0.29	0.6	14	0.55
Weather (PC1)	0.1	0.07	250	1.47	0.14
Treatment (Cortisol)					
<i>Females</i>	-0.15	0.33	-0.46	14	0.65
<i>Males</i>	-0.06	0.28	-0.22	7	0.83
<b>Sex (M) x Age</b>	<b>-0.48</b>	<b>0.18</b>	<b>-2.69</b>	<b>230</b>	<b>0.008</b>
Sex (M) x Foraging success	-0.14	0.14	-1.02	395	0.3
Sex (M) x Treatment (Cortisol)	0.09	0.34	0.26	18	0.79
<b>Age x Treatment (Cortisol)</b>					
<i>Females</i>	<b>-0.65</b>	<b>0.22</b>	<b>-2.95</b>	<b>481</b>	<b>0.0033</b>
<i>Males</i>	-0.07	0.15	-0.49	507	0.62
Group size x Pups Present (Yes)	-0.17	0.12	-1.39	272	0.17
Group size2 x Pups Present (Yes)	0.11	0.12	488	0.96	0.34
Group size x Weather (PC1)	0.06	0.06	1	202	0.32
<b>Age x Sex (M) x Treatment (Cortisol)</b>	<b>0.57</b>	<b>0.25</b>	<b>2.3</b>	<b>456</b>	<b>0.022</b>

Data used in these analyses were 542 faecal samples (n= 355 from controls, n = 187 from cortisol treated litters) from 34 subordinate meerkats (control: n = 12 females, n = 11 male2; cortisol-treated: n = 5 females, n = 6 males) produced in 10 litters from 7 different groups. Reference levels (intercept) for “Sex” was female, “Pups in group” was Yes, and for Relatedness was “No parent was dominant”.