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## Live long and prosper: durable benefits of early life care in banded mongooses

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4 1 **Live long and prosper: durable benefits of early life care in**  
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## 27 **ABSTRACT**

28 Kin selection theory defines the conditions for which altruism or ‘helping’ can be favoured by  
29 natural selection. Tests of this theory in cooperatively breeding animals have focused on the  
30 short-term benefits to the recipients of help, such as improved growth or survival to  
31 adulthood. However, research on early life effects suggests that there may be more  
32 durable, lifelong fitness impacts to the recipients of help, which in theory should strengthen  
33 selection for helping. Here we show in cooperatively breeding banded mongooses (*Mungos*  
34 *mungo*) that care received in the first three months of life has lifelong fitness benefits for  
35 both males and female recipients. In this species adult helpers called ‘escorts’ form  
36 exclusive one-to-one caring relationships with specific pups (not their own offspring),  
37 allowing us to isolate the effects of being escorted on later reproduction and survival. Pups  
38 that were more closely escorted were heavier at sexual maturity, which was associated with  
39 higher lifetime reproductive success for both sexes. Moreover, for female offspring, lifetime  
40 reproductive success increased with the level of escorting received *per se*, over and above  
41 any effect on body mass. Our results suggest that early life social care has durable benefits  
42 to offspring of both sexes in this species. Given the well-established developmental effects  
43 of early life care in lab animals and humans, we suggest that similar effects are likely to be  
44 widespread in social animals more generally. We discuss some of the implications of  
45 durable fitness benefits for the evolution of intergenerational helping in cooperative animal  
46 societies, including humans.

## 49 **1. INTRODUCTION**

50 Social evolution theory aims to understand and predict how natural selection acts on  
51 heritable social traits, that is, traits that affect the fitness of other members of a population.  
52 Hamilton’s [1, 2] inclusive fitness theory defined the condition ( $r b > c$ , known as Hamilton’s  
53 rule) for which selection can favour the evolution of altruism (i.e. a trait that boosts the  
54 lifetime fitness  $b$  of a recipient, related by coefficient  $r$ , at a lifetime fitness cost  $c$  to the  
55 actor) directed toward genetic relatives. Subsequent theory has emphasised repeated  
56 interactions, intergroup competition, and group augmentation as promoters of cooperative  
57 behaviour[3-5]. Inclusive fitness theory in particular has provided a very general framework  
58 to understand variation in social traits (both behavioural and life history traits), and to  
59 identify ecological and demographic factors that facilitate cooperation and the formation of  
60 animal societies[6, 7].

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62 Cooperative animal societies, in which ‘helpers’ work to rear offspring that are not their own,  
63 are a rich testing ground for these theories because they feature conspicuous examples of

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3 64 altruism or 'helping', together with the possibility of measuring the fitness consequences of  
4 65 variation in helping effort and life history decisions. In addition, research on cooperative  
5 66 vertebrates provides a potentially informative comparator for *Homo sapiens*, one of the few  
6 67 cooperatively breeding primates [9, 10]. There is now considerable evidence that major  
7 68 features of human life history (e.g. long period of offspring dependency, short inter-birth  
8 69 interval, early reproductive cessation, prolonged post-reproductive lifespan) have been  
9 70 moulded via kin selection operating in the family groups of our Pleistocene ancestors [11-  
10 71 16].  
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18 73 Although the costs and benefits in Hamilton's rule are in the currency of lifetime direct  
19 74 fitness, tests of kin selection theory and other proposed mechanisms of cooperation (such  
20 75 as reciprocity and coercion[17, 18]) rely on measuring reasonable proxies for lifetime fitness  
21 76 impacts. For example, the fitness benefit conferred by helpers might be tested by  
22 77 comparing the number of surviving offspring produced by reproductives with and without the  
23 78 assistance of helpers [12, 19, 20]. But the literature on early life effects and developmental  
24 79 plasticity shows that there may often be delayed impacts of investment that are manifested  
25 80 long after the initial act. In social insects, for example, variation in provisioning in the larval  
26 81 period triggers developmental switches and leads to permanent behavioural and  
27 82 morphological castes[21, 22]. In vertebrates permanent castes are typically lacking, but  
28 83 research on lab rodents and humans shows that postnatal care can have lifelong effects on  
29 84 cognitive function, social behaviour and health [23-25]. Thus the effects of help on a  
30 85 recipient's fitness, particularly when the recipients is an individual offspring, may be  
31 86 manifested long after the helping act itself – even after the helper has died or dispersed..  
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42 88 The potential for early life investment to 'program' an offspring's subsequent life history  
43 89 could promote or inhibit selection for helping, depending on whether helped offspring are  
44 90 more or less likely to disperse, and more or less likely to produce surviving offspring  
45 91 themselves. These delayed impacts of help represent an 'internal' durable benefit conferred  
46 92 by the helper, similar to the 'external' durable benefits that can arise through niche  
47 93 construction, for example, the construction of a nest or shelter that benefits future  
48 94 generations. Recent theory suggests that the potential for helping to result in benefits that  
49 95 are manifested in the future (in addition to, or instead of, fitness benefits that are manifested  
50 96 contemporaneously with the helping act), has a strong influence on selection for altruism in  
51 97 structured populations [26]. In these 'patch-structured' or 'group-structured' models, helping  
52 98 boosts the fecundity (number of offspring) of the local group of kin, but also increases  
53 99 competition among these local kin. The former inclusive fitness benefit of helping is  
54 100 counteracted by the latter inclusive fitness cost resulting from increased competition. The

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3 101 further into the future the benefits of helping are realised, the lower the relatedness of the  
4 102 actor to the individuals in the patch that suffer the costs of competition, and hence the  
5 103 greater the overall strength of selection for helping [26].  
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9 105 The potential durable benefits of helping in cooperative animal societies have been little  
10 106 explored empirically. One exception is Russell et al's [27] study of meerkats (*Suricata*  
11 107 *suricatta*) which showed that female offspring that gain most weight during the helping  
12 108 period (and hence are likely to have received more help), and those that are experimentally  
13 109 fed, are more likely to reproduce at some point in their lives and more likely to attain the  
14 110 position of dominant breeder. In other cooperatively breeding vertebrates (including  
15 111 humans), measuring delayed or lifelong impacts of help is challenging because it requires  
16 112 following the recipients of care across their entire lifespan, and recipients often die or  
17 113 disperse before attaining reproductive status.  
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25 115 Here we investigate the immediate and lifelong consequences for the recipients of helping  
26 116 in a cooperatively breeding mammal, the banded mongoose (*Mungos mungo*), using a 17  
27 117 year dataset. This species exhibits an unusual form of one-to-one early life offspring care  
28 118 called 'escorting' which provides an opportunity to tease apart genetic, maternal, and  
29 119 alloparental effects on development and later life history [28, 29]. Multiple females give birth  
30 120 in each breeding attempt, usually on the same day [30], and the communal litter is kept  
31 121 underground for the first month of life. Mothers show no discrimination during suckling, and  
32 122 pups are sometimes observed to move from female to female to suckle [31, 32]. From the  
33 123 time that pups emerge from the den until they reach nutritional independence at 3 months  
34 124 old, pups form exclusive one-to-one caring relationships with adult helpers (their 'escorts')  
35 125 who are no more closely related than a random group member [28]. Escorts provision and  
36 126 groom the pups in their care, and carry them away from danger. However, there is great  
37 127 variation among offspring in the amount of escorting received: some pups spend all day  
38 128 every day with their escort, whereas others have to fend for themselves from an early age  
39 129 [28, 29].  
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50 131 The escort system allows us to quantify the amount of post-natal help received by individual  
51 132 offspring in each communal litter. By contrast, in most other cooperatively breeding insects,  
52 133 birds and mammals, helper effort is shared across entire litters or broods [33], so it is more  
53 134 difficult to isolate the fitness impacts of the investment by an individual helper on an  
54 135 individual recipient. In addition, our system is unusual because dispersal away from the  
55 136 study site is rare [34, 35], and we can follow individuals across their entire lives, from pup to  
56 137 reproducing adult. In this paper we capitalise on this system to test whether the care  
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3 138 received by pups in the first three months of life has lasting effects on their survival and  
4 139 reproduction as adults, long after the period of care has ended.

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## 9 142 **2. MATERIALS AND METHODS**

### 11 143 **(a) Study species & population**

12 144 Banded mongooses are small (1.5kg) cooperatively breeding carnivorous mammals  
13 145 common to sub-Saharan Africa. Since 1995 we have continuously studied a habituated  
14 146 population of wild banded mongooses living on and around the Mweya peninsula in Queen  
15 147 Elizabeth National Park, western Uganda (0 12' S, 29 54'E); for details of the field site and  
16 148 the population, see [36] and references therein. At any one time the population consists of  
17 149 8-12 mixed sex groups of 10 to 30 individuals, plus offspring. On average four females give  
18 150 birth in each breeding attempt, synchronising birth to the same day in 64% of breeding  
19 151 attempts [30]. The resulting mixed-parentage litter of pups is guarded at the den during the  
20 152 first month of life by one or more babysitters [36]. After emergence care is provided by  
21 153 escorts up to the age of 3 months [28, 37]. Individuals reach sexual maturity at around 1  
22 154 year old, and life expectancy at this age is around 3 years (males = 42 months; females =  
23 155 38 months. There is no reproductive suppression among females in this species: adult  
24 156 females start breeding when they are 1 year old and produce up to four litters per year until  
25 157 they die [34]. Males, by contrast, form an age-based social queue in which the oldest two or  
26 158 three individuals mate-guard and aggressively monopolise access to oestrous females [38,  
27 159 39] Younger males, though sexually mature, are typically excluded from reproduction until  
28 160 they reach relatively advanced ages (3+ years; [39]).

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30 162 We collected data from individuals from 12 social groups of on average 22 adult individuals  
31 163 (SD 7.3, range 7-37) inhabiting the study area between the years 2000-2016. All  
32 164 mongooses in the study population are individually marked using either unique hair-shave  
33 165 patterns or colour-coded collars, and are habituated to close observation from at least 5m.  
34 166 Additionally each mongoose is marked with a transponder chip (Wyre micro design, UK) or,  
35 167 before the year 2009, with a unique tattoo on the inside of the leg. One to two mongooses  
36 168 in each group are fitted with a radio collar weighing 26 to 30 g (Sirtrack Ltd, Havelock North,  
37 169 New Zealand) to allow the groups to be located.

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### 39 171 **(b) Life history parameters and genotyping**

40 172 Over the 17 year study period each group was visited for at least 20 minutes every 1-3 days  
41 173 to record presence and absence of individuals in each group. As banded mongooses  
42 174 almost always disperse in groups, either voluntarily or through a process of violent eviction

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3 175 [40-42], we could distinguish between dispersal and deaths as cause for permanent  
4 176 absence from the group. For the dataset used in the analyses, we included only those  
5 177 individuals whose date of birth and death were both known with at least one weeks'  
6 178 accuracy.  
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11 180 We identified female pregnancy by visual swelling of the abdomen and confirmed this by  
12 181 palpation and ultrasound scans during trapping [43]. Births occur overnight in an  
13 182 underground den, and were identified by the absence of pregnant females the following  
14 183 morning and a subsequent change in their body shape and mass loss [30, 44]. Pups were  
15 184 first captured at emergence from the den, at around 3-4 weeks of age, weighed and sexed,  
16 185 and given a unique ID; see [45] for further details of the trapping procedure. When  
17 186 individuals were first trapped, a 2-mm skin sample was taken for extraction of DNA, which  
18 187 was used to construct a pedigree for assigning parentage. Parentage was assigned using  
19 188 Masterbayes 2.51 [46] and COLONY 2.0.5.7 [47] as described in [48], for a dataset of 2310  
20 189 individuals born in the study area between the years 2000 and 2016. Lifetime reproductive  
21 190 success was determined as the total number of pups assigned to each individual. For full  
22 191 details of DNA extraction, genotyping, parentage assignment and pedigree construction see  
23 192 [48, 49].  
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### 33 194 **(c) Measuring early-life care**

34 195 Shortly after emergence from the den, pups form one-to-one caring relationships with  
35 196 particular adults known as 'escorts', that feed, carry, groom and protect the pup from  
36 197 predators [37]. The majority of pups have an exclusive relationship with a single escort;  
37 198 where pups have multiple escorts, they spend the great majority of their time with a single  
38 199 'primary' escort [29]. Escorting starts at around 4 weeks of age and continues until pups  
39 200 reach nutritional independence, when they are around 90 days old (hereafter defined as the  
40 201 'escorting period'). While pup-escort dyads are forming, pups aggressively defend access to  
41 202 their escort [50], but thereafter both parties (escort and pup) actively seek each other out to  
42 203 maintain the association [51]. Experiments demonstrate that escorts and pups can  
43 204 recognise each other's calls, and that escorts are particularly reactive to the distress calls of  
44 205 the specific pup in its care [51, 52].  
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53 207 We observed escorting behaviour in 120 communal litters in 12 social groups that inhabited  
54 208 the study area between 2000-2016. Groups were visited an average of 12 times during the  
55 209 escorting period, for a minimum of 20 minutes (the duration of one pup focal observation  
56 210 session). Only those litters for which we had five or more observation sessions (on different  
57 211 days) were included in the analyses. Pup focals were conducted so that each pup was



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3 212 followed for 20 minutes, and at each minute interval, individuals within 30cm of the focal  
4 213 individual were noted (focals were paused if the focal pup went out of sight, and resumed  
5 214 once sighted again). If the pup spent more than half of the 20 minute focal within 30cm of  
6 215 the same individual, that adult was marked as the escort for that focal session [28]. The  
7 216 proportion of the pup focals a pup was seen being escorted was taken as a measure of  
8 217 care it received, termed its 'escorting index'. Consequently the escort index varies from 0  
9 218 (never observed being escorted) to 1 (always observed being escorted).

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#### 16 220 **(d) Body mass and ecological data**

17 221 The emergence body mass of pups was recorded when the pups were first trapped at 3-4  
18 222 weeks of age, see above. Adult body mass measurements were collected as part of the  
19 223 group visits. Most individuals are trained to step onto portable weighing scales in return for  
20 224 a small milk reward and were weighed weekly in the morning before foraging started.

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25 226 Climate data was collected by Mweya meteorological station, and after 2014 by the Banded  
26 227 Mongoose Research Project. Cumulative rainfall during the month before the litter was born  
27 228 was used as a proxy of resource availability, as previous studies indicate that rainfall in the  
28 229 previous 30 days is positively correlated with adult daily body mass gain and pregnancy rate  
29 230 [53, 54]).

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#### 35 232 **(e) Statistical analyses and model selection**

36 233 *Immediate survival and post-escorting survival to one year.* We used Generalised Linear  
37 234 Mixed Models (GLMMs) with a binomial error structure and logit link function, to analyse  
38 235 predictors of survival to nutritional independence at 3 months, and survival to maturity at  
39 236 one year. Predictor variables were escorting index, emergence weight of the pup,  
40 237 cumulative rainfall in the month before birth, and sex of the pup. An interaction between sex  
41 238 and escorting index was included to test for differential effects of escorting between the  
42 239 sexes. Social group ID and communal litter ID into which the pup was born were included  
43 240 as random factors in the analyses. This allows the intercept of the model to vary by litter ID  
44 241 and group, to control for group-level and litter specific factors.

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52 243 *Body mass.* We used a linear mixed model (LMM) to look at predictors of body mass at one  
53 244 year. The model included predictor and random factors as above.

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57 246 *Age at maturity.* We used linear mixed models (LMM) to investigate the age at which first  
58 247 signs of reproductive activity were observed in females (first oestrus), and males (the first  
59 248 mate guarding or 'pestering' behaviour during group oestrus [34]). As the definition for the



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3 249 start of reproduction is different, the sexes were analysed separately, but otherwise both  
4 250 models included predictor and random factors as above (escorting index, emergence weight  
5 251 of the pup, rainfall during month before birth as predictors, and social group and litter as  
6 252 random factors).

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11 254 *Adult lifespan.* Rainfall, weight at emergence, escorting index, sex of the individual and the  
12 255 interaction between sex and escorting index were included as predictors in a LMM of total  
14 256 lifespan, and litter and pack included as random factors.

16 257 *Lifetime reproductive success.* In analyses of lifetime reproductive success, the total  
17 258 number of offspring was first fitted as the response variable in a GLMM with a Poisson error  
18 259 structure and a log link function. The sexes were analysed separately to improve model  
20 260 convergence. Emergence weight, escorting index, rainfall and weight at maturity were  
21 261 included as predictors, and litter and group as random factors. We then fitted the same  
22 262 models again, but using the log (total lifespan of the individual) as an offset in the model, to  
23 263 analyse whether the included variables predicted the *rate* at which individuals produced  
24 264 offspring by accounting for differences in lifespan.

26 265 In all analyses, weights and rainfall were standardised by subtracting the mean and dividing  
27 266 by standard deviation, to improve model convergence. The correlation of predictor variables  
28 267 in each analysis was checked to confirm that it was not high enough to cause model fitting  
29 268 issues [55]. Nonsignificant interactions were dropped to allow significance testing of main  
30 269 terms [56], but models were not simplified further [57]. In the analyses that involved fitting  
31 270 models with a normal error structure (body mass, age at maturity and adult lifespan) we  
32 271 visually checked the residuals to ensure they met the model assumptions of normally  
33 272 distributed residuals with homogeneous variance. Where necessary we log-transformed the  
34 273 response variable (body mass and adult lifespan) to meet these assumptions.

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46 275 Statistical analyses were done in R version 3.3.1 [58] and GLMM models fitted using R  
47 276 package lme4 [59]. The significance of predictor variables was determined by performing  
48 277 likelihood ratio tests comparing the full model to a model without the predictor variable,  
49 278 removing non-significant interactions to allow the main effects of variables involved in these  
50 279 interactions to be assessed [60]. We report the  $\chi^2$  statistics and parameter estimates ( $\beta \pm$   
51 280 SE) for significant terms, and the full analysis results including non-significant parameter  
52 281 estimates are presented in the Supplementary Information tables S1-S3.

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### 3. RESULTS

**(a) Developmental impacts of early life care**

*Immediate survival.* Pups that received more care were more likely to survive until nutritional independence, as were those that were heavier at emergence (binomial GLMM: emergence weight:  $\beta = 0.83 \pm 0.15$ ,  $\chi^2_1 = 36.44$ ,  $p < 0.00001$ ; Table S1). Pup survival was higher in periods of higher rainfall ( $\beta = 0.51 \pm 0.18$ ,  $\chi^2_1 = 8.66$ ,  $p = 0.003$ ), whereas the sex of the pup had no effect ( $\beta = -0.16 \pm 0.22$ ,  $\chi^2_1 = 0.57$ ,  $p = 0.45$ ).

*Post-escorting survival to one year.* Beyond the escorting period, care received did not predict survival to maturity at one year of age (binomial GLMM: escorting index: ( $\beta = 0.11 \pm 0.43$ ,  $\chi^2_1 = 0.06$ ,  $p = 0.802$ ; Table S1). Males were more likely to survive to maturity ( $\beta = 0.50 \pm 0.24$ ,  $\chi^2_1 = 4.38$ ,  $p = 0.036$ ) whereas rainfall had no effect ( $\beta = 0.21 \pm 0.14$ ,  $\chi^2_1 = 2.05$ ,  $p = 0.152$ ).

*Body mass at maturity.* Pups that received more care during the escorting period were heavier at one year of age, as were those that were heavier at emergence (Figure 2; LMM, pups that survived to 12 months only: escorting index:  $\beta = 89.0 \pm 33.5$ ,  $\chi^2_1 = 6.85$ ,  $p = 0.009$ ; emergence weight:  $\beta = 52.7 \pm 11.8$ ,  $\chi^2_1 = 18.9$ ,  $p < 0.001$ ; for full model details see Table 1).

*Age at maturity.* Female pups that received more care had their first oestrus earlier (LMM, pups that survived to 12 months only: escorting index:  $\beta = -0.34 \pm 0.15$ ,  $\chi^2_1 = 5.16$ ,  $p = 0.023$ ). None of the tested variables predicted the timing of first observed mate guarding behaviour in males (all  $p > 0.2$ , see Table S2).

**(b) Lifetime impacts of early life care**

*Effects on adult lifespan.* Adult lifespan was not longer for individuals that received more care as pups (escorting index:  $\beta = -0.03 \pm 0.13$ ,  $\chi^2_1 = 0.06$ ,  $p = 0.81$ ; all other variables  $p > 0.098$ , see Table S3).

*Effects on lifetime reproductive success.* Females that received more care as pups had higher lifetime reproductive success (Figure 2A; escort index:  $\beta = 1.691 \pm 0.56$ ,  $\chi^2_1 = 12.39$ ,  $p = 0.0004$ ), as did those that experienced heavier rainfall during the first month of life ( $\beta = 0.51 \pm 0.24$ ,  $\chi^2_1 = 4.91$ ,  $p = 0.027$ ) and that were heavier at maturity (weight at one year:  $\beta = 0.48 \pm 0.20$ ,  $\chi^2_1 = 4.3$ ,  $p = 0.038$ ). When using lifespan as an offset, the amount of care and weight at one year were the only significant predictors of a female's lifetime reproductive success (see Table 1). Thus, female pups that received more care in early life

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3 321 had greater lifetime reproductive success because they produced surviving offspring at a  
4 322 higher rate across their lifespan, not because they lived longer. Of the female pups that  
5 323 survived to adulthood, those that had been lighter at emergence had higher lifetime  
6 324 reproductive success ( $\beta = -0.46 \pm 0.19$ ,  $\chi^2_1 = 5.69$ ,  $p = 0.017$ ; although not when using  
7 325 lifespan as an offset; see Table S3). This unexpected finding may reflect selective  
8 326 disappearance during development (e.g. [61]): most lightweight pups die before reaching  
9 327 adulthood, so those lightweight pups for which we have a measure of lifetime reproductive  
10 328 success may represent a special subset of high quality or high-survivorship individuals,  
11 329 compared to pups for which early life mortality is less severe (Table S1).

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12 331 In males there was no significant effect of early life care on lifetime reproductive success  
13 332 (Figure 2B;  $\beta \pm SE = -0.39 \pm 0.56$ ,  $\chi^2_1 = 0.49$ ,  $p = 0.48$ ). The only significant predictor of  
14 333 male lifetime reproductive success was body mass at one year, with males that were  
15 334 heaviest at maturity gaining highest lifetime reproductive success ( $\beta \pm SE = 0.75 \pm 0.23$ ,  $\chi^2_1 =$   
16 335  $11.03$ ,  $p = 0.0009$ ; all other variables  $p > 0.3$ : Table 1). Results were similar when using  
17 336 lifespan as an offset, and the only significant predictor of male lifetime reproductive success  
18 337 was mass at one year (Table 1).

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#### 340 4. DISCUSSION

341 Our results suggest that early life care directed by escorts to specific offspring has both  
342 immediate survival benefits and durable fitness benefits that are manifested across the  
343 offspring's subsequent lifespan. The immediate survival benefits are expected because  
344 adult escorts and pups stay in close proximity throughout the day, and escorts are quick to  
345 alert, defend and carry their pup away from danger. The durable fitness benefits of being  
346 escorted are striking and manifested in two ways. First, for both male and female pups,  
347 escorting had a durable impact on body mass at maturity, which is positively associated  
348 with lifetime reproductive success in both sexes. In addition, independent of any effect on  
349 body mass, female pups that received higher levels of escorting were more efficient at  
350 producing surviving offspring and had higher lifetime reproductive success compared to  
351 females that received little escorting.

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353 The presence of these durable fitness benefits to the recipients of early life care is  
354 consistent with numerous findings from laboratory studies which suggest that the quality of  
355 parental care received in early life can have a profound impact on adult physiology, health  
356 and behaviour. In a classic laboratory study of Long-Evans hooded rats, offspring that  
357 received more licking and grooming from their mothers in the first ten days of life showed

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3 358 reduced hypothalamic-pituitary-adrenal (HPA) endocrinological stress reactivity as adults  
4 359 [62]. Moreover, those (female) offspring were also more likely to express high levels of  
5 360 nurturing behaviour when they became mothers themselves, suggesting that early life care  
6 361 can produce a chain of behavioural effects and potential benefits to recipients that last  
7 362 generations into the future. The transgenerational inheritance of grooming/licking behaviour  
8 363 in rats has a well-established epigenetic basis [63]. If such mechanisms operate in natural  
9 364 populations, cooperative care directed at offspring could have self-reinforcing or even  
10 365 runaway effects on levels of local helping (in the case where helped offspring are more  
11 366 likely to provide help themselves); or self-limiting effects (if helped offspring are less likely to  
12 367 provide help at a later date). The potential for transgenerational impacts of cooperation are  
13 368 rendered plausible by the detailed mechanistic work on laboratory rodents, and are a fruitful  
14 369 area for both theoretical and empirical research. One of our future aims is to use the  
15 370 unusual escort system to investigate possible transgenerational influences on individual  
16 371 cooperative behaviour in this system.

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27 373 In our study only female offspring experienced an additional lifetime fitness benefit of being  
28 374 escorted *per se*, over and above any effect on body mass. This sex difference may reflect  
29 375 differences in the sensitivity of female and male reproductive systems to the conditions  
30 376 experienced in development, or sex differences in the key physical attributes (e.g. body size  
31 377 versus stress physiology) linked to reproductive success. It may also reflect a unisexual  
32 378 pattern of epigenetic inheritance of maternal-care-like behaviour. In the rat studies, both  
33 379 male and female offspring showed similar impacts of being licked/groomed on HPA  
34 380 reactivity and development, but only mothers provide care in this system, and hence only  
35 381 daughters inherited an elevated propensity to lick/groom their own offspring [64]. A third  
36 382 factor in banded mongooses is that there is a sex difference in the time delay to the  
37 383 realisation of any durable benefit: males form a strict dominance hierarchy and must wait  
38 384 much longer to start reproducing compared to females (3+ years versus 1 year for females;  
39 385 [34]), so any durable benefits of being escorted as a pup may become diluted by other  
40 386 factors (environmental and/or social) that impinge on male lifetime reproductive success in  
41 387 the interim.

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52 389 Theoretical analyses of durable impacts of help have focused on external benefits that arise  
53 390 through niche construction or the production of durable physical objects and structures [26].  
54 391 Our findings suggest that durable benefits can also arise through development, for example,  
55 392 because recipients of help are protected from external insults or stressors during sensitive  
56 393 developmental windows, or are able to carry over extra resources to adulthood [27].  
57 394 Lehmann's [26] model predicts that where the benefits of help are separated in time from

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3 395 the act of helping, selection for helping is strengthened (other things being equal). Selection  
4 396 for helping is particularly strong where benefits are realised after the actor has died or  
5 397 ceased reproduction, and is therefore unable to experience any negative effects of the  
6 398 increase in local competition resulting from the helping act. Thus we can predict that where  
7 399 helping results in 'internal' durable benefits, selection for helping should increase with  
8 400 helper age, since older helpers are less likely to suffer direct competition from offspring  
9 401 produced as a result of their help. In humans, killer whales, and elephants, grandmothers  
10 402 have demonstrable positive impacts on the reproductive success of their offspring [11, 12,  
11 403 65-67]. However, these and other studies typically assume that any benefits associated with  
12 404 grandmother presence cease upon her death; whereas our study suggests that the impact  
13 405 of care may persist long after a helper has died. Durable benefits might go some way  
14 406 toward explaining why, in humans, many analyses have found that the (immediate)  
15 407 measurable fitness benefits of grandmothing are too small to favour the evolution of  
16 408 menopause ([68, 69]; but see [13]).  
17 409

18 410 Both our study and studies of grandmothing are examples where it is natural to assume  
19 411 that the recipients of help are members of a younger generation, such as young offspring or  
20 412 younger breeders. By contrast, most studies of cooperative breeding focus on the impact of  
21 413 help on the reproductive success of breeding adults, rather than their offspring [33]. In  
22 414 principle, Hamilton's rule could be utilised to determine the direction of selection on genes in  
23 415 parents or in their offspring – what matters in each case is correct consideration of genetic  
24 416 relatedness and recipient reproductive value (e.g. [70]). In banded mongooses it is natural  
25 417 to view individual offspring as the recipients of help, not their parents, since each offspring  
26 418 is the sole benefactor of the care provided by escorts, while the other offspring of the parent  
27 419 are cared for by other individuals. In other cooperative breeders, it is more practical to focus  
28 420 on parental fitness because help is provided to multiple offspring at a time, and it is difficult  
29 421 to track the impact of help on the reproductive success of all these younger recipients  
30 422 across their life course. However, our study suggests that an exclusive focus on parental  
31 423 reproductive success (measured as their number of surviving young) does not take account  
32 424 of any durable benefits of help and hence may systematically underestimate the strength of  
33 425 selection for altruism in natural systems.  
34 426

35 427 In conclusion, our multigenerational study of a cooperative mammal living in the  
36 428 environment in which it evolved suggests that helping has lifelong fitness impacts on both  
37 429 male and female offspring. These durable fitness benefits may be challenging to detect and  
38 430 measure, particularly in long-lived species. Nevertheless, the extensive literature on early  
39 431 life effects gives reason to believe that durable impacts may be widespread and can be

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3 432 expected to have major impacts on social evolution and life history. Further theoretical  
4 433 research is needed to investigate when durable benefits will result in positive or negative  
5 434 feedback between care received and helping effort in cooperative societies, and the  
6 435 consequences for social evolution. Further empirical research is needed to test for these  
7 436 effects in wild animal societies; and investigate whether such early life effects in natural  
8 437 systems are mediated by epigenetic and neuroendocrinological changes similar to those  
9 438 observed in lab mammals.

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#### 17 441 **ETHICAL STATEMENT**

18 442 All research was carried out under permit from Uganda Wildlife Authority (UWA) and  
19 443 Uganda National Council for Science and Technology (UNCST). All procedures adhered to  
20 444 the Guidelines for the Treatment of Animals in Behavioural Research and Teaching,  
21 445 published by the Association for the Study of Animal Behaviour, and received prior approval  
22 446 from UWA, UNCST, and the Ethical Review Board of the University of Exeter.

27 447

#### 28 448 **DATA ACCESSIBILITY**

29 449 The data supporting the analyses will be deposited online and made freely available on  
30 450 Figshare on publication of this paper.

33 451

#### 34 452 **COMPETING INTERESTS**

35 453 The authors declare no competing interests.

38 454

#### 39 455 **AUTHOR CONTRIBUTIONS**

40 456 E.V. and M.C. designed research; E.V., H.M., F.T. collected data; M.C. managed the field  
41 457 project; E.V. and F.T. analysed data; F.T. prepared the figures; M.C. and E.V. wrote the first  
42 458 draft; all authors contributed to the final version.

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55  
56  
57  
58  
59  
60

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2  
3 482 **REFERENCES**

- 4  
5 483 [1] Hamilton, W. D. 1963 The evolution of altruistic behavior. *American Naturalist* **97**, 354-  
6 484 365.
- 7  
8  
9 485 [2] Hamilton, W. D. 1964 The genetical evolution of social behaviour. *Journal of Theoretical*  
10 486 *Biology* **7**, 1-16.
- 11  
12  
13 487 [3] Nowak, M. A. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560-1563.
- 14  
15 488 [4] Choi, J.-K. & Bowles, S. 2007 The coevolution of parochial altruism and war. *Science*  
16 489 **318**, 636-640.
- 17  
18  
19 490 [5] Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative  
20 491 breeding through group augmentation. *Proceedings of the Royal Society of London*  
21 492 *Series B* **268**, 187-196.
- 22  
23  
24 493 [6] Gardner, A., West, S. A. & Wild, G. 2011 The genetical theory of kin selection. *Journal of*  
25 494 *Evolutionary Biology* **24**, 1020-1043.
- 26  
27  
28 495 [7] Lehmann, L. & Rousset, F. 2010 How life history and demography promote or inhibit the  
29 496 evolution of helping behaviours. *Philosophical Transactions of the Royal Society B*  
30 497 **365**, 2599-2617.
- 31  
32  
33 498 [8] Hamilton, W. D. 1966 The moulding of senescence by natural selection. *Journal of*  
34 499 *Theoretical Biology* **12**, 12-45.
- 35  
36  
37 500 [9] Mace, R. & Sear, R. 2005 Are humans cooperative breeders? In *Grandmotherhood: the*  
38 501 *Evolutionary Significance of the Second Half of Female Life* (eds. E. Voland, A.  
39 502 Chasiotis & W. Schiefenhoevel), pp. 143-159. Piscataway, N.J., Rutgers University  
40 503 Press.
- 41  
42  
43 504 [10] Burkart, J. M., Hrdy, S. B., & Van Schaik, C. P. 2009. Cooperative breeding and human  
44 505 cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, **18**,  
45 506 175-186.
- 46  
47  
48 507 [11] Hawkes, K., O'Connell, J. F., Blurton-Jones, N. G., Alvarez, H. & Charnov, E. L. 1998  
49 508 Grandmothering, menopause, and the evolution of human life histories. *Proceedings*  
50 509 *of the National Academy of Sciences of the United States of America* **95**, 1336-  
51 510 1339.
- 52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 511 [12] Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. 2004 Fitness  
4 512 benefits of prolonged post-reproductive lifespan in women. *Nature* **428**, 178-181.  
5  
6  
7 513 [13] Cant, M. A. & Johnstone, R. A. 2008 Reproductive conflict and the separation of  
8 514 reproductive generations in humans. *Proceedings of the National Academy of*  
9 515 *Sciences of the United States of America* **105**, 5332-5336.  
10  
11  
12 516 [14] Jones, N. B. 2016 *Demography and evolutionary ecology of Hadza hunter-gatherers*,  
13 517 Cambridge, Cambridge University Press.  
14  
15  
16 518 [15] Lahdenperä, M., Gillespie, D. O., Lummaa, V. & Russell, A. F. 2012 Severe  
17 519 intergenerational reproductive conflict and the evolution of menopause. *Ecology*  
18 520 *Letters* **15**, 1283-1290.  
19  
20  
21 521 [16] Mace, R. & Alvergne, A. 2012 Female reproductive competition within families in rural  
22 522 Gambia. *Proceedings of the Royal Society of London B*, rspb20112424.  
23  
24  
25 523 [17] Raihani, N. J., Thornton, A. & Bshary, R. 2012 Punishment and cooperation in nature.  
26 524 *Trends in Ecology and Evolution* **27**, 288-298.  
27  
28  
29 525 [18] Cant, M. A. 2011 The role of threats in animal cooperation. *Proceedings of the Royal*  
30 526 *Society B* **278**, 170-178.  
31  
32  
33 527 [19] Komdeur, J. 1994 Experimental-Evidence for Helping and Hindering by Previous  
34 528 Offspring in the Cooperative-Breeding Seychelles Warbler *Acrocephalus-*  
35 529 *Sechellensis*. *Behavioral Ecology and Sociobiology* **34**, 175-186.  
36  
37  
38 530 [20] Hatchwell, B. J., Russell, A. F., MacColl, A. D. C., Ross, D. J., Fowlie, M. K. &  
39 531 McGowan, A. 2004 Helpers increase long-term but not short-term productivity in  
40 532 cooperatively breeding long-tailed tits. *Behavioral Ecology* **15**, 1-10.  
41  
42  
43 533 [21] Oster, G. F. & Wilson, E. O. 1979 *Caste and ecology in the social insects*, Princeton,  
44 534 Princeton University Press.  
45  
46  
47 535 [22] Schwander, T., Lo, N., Beekman, M., Oldroyd, B. P. & Keller, L. 2010 Nature versus  
48 536 nurture in social insect caste differentiation. *Trends in Ecology and Evolution* **25**,  
49 537 275-282.  
50  
51  
52 538 [23] Cameron, N. M., Shahrokh, D., Del Corpo, A., Dhir, S. K., Szyf, M., Champagne, F. A.  
53 539 & Meaney, M. J. 2008 Epigenetic programming of phenotypic variations in  
54 540 reproductive strategies in the rat through maternal care. *Journal of*  
55 541 *Neuroendocrinology* **20**, 795-801.  
56  
57  
58  
59  
60

- 1  
2  
3 542 [24] van der Horst, F. C. P. & van der Veer, R. 2008 Loneliness in Infancy: Harry Harlow,  
4 543 John Bowlby and Issues of Separation. *Integrative Psychological and Behavioral*  
5 544 *Science* **42**, 325-335.  
6  
7  
8  
9 545 [25] Black, M. M., Walker, S. P., Fernald, L. C. H., Andersen, C. T., DiGirolamo, A. M., Lu,  
10 546 C., McCoy, D. C., Fink, G., Shawar, Y. R., Shiffman, J., et al. 2017 Early childhood  
11 547 development coming of age: science through the life course. *The Lancet* **389**, 77-90.  
12  
13  
14 548 [26] Lehmann, L. 2007 The evolution of trans-generational altruism: kin selection meets  
15 549 niche construction. *Journal of Evolutionary Biology* **20**, 181-189.  
16  
17  
18 550 [27] Russell, A., Young, A., Spong, G., Jordan, N. & Clutton-Brock, T. 2007 Helpers  
19 551 increase the reproductive potential of offspring in cooperative meerkats.  
20 552 *Proceedings of the Royal Society of London B* **274**, 513-520.  
21  
22  
23  
24 553 [28] Vitikainen, E. I. K., Marshall, H. H., Thompson, F. J., Sanderson, J. L., Bell, M. B. V.,  
25 554 Gilchrist, J. S., Hodge, S. J., Nichols, H. J. & Cant, M. A. 2017 Biased escorts:  
26 555 offspring sex, not relatedness explains alloparental care patterns in a cooperative  
27 556 breeder. *Proceedings of the Royal Society of London B* **284**, 20162384  
28  
29  
30  
31 557 [29] Sheppard, C. E., Marshall, H. H., Inger, R., Thompson, F. J., Vitikainen, E. I., Barker,  
32 558 S., Nichols, H. J., Wells, D. A., McDonald, R. A. & Cant, M. A. 2018 Decoupling of  
33 559 genetic and cultural inheritance in a wild mammal. *Current Biology* **28**, 1846-1850.  
34  
35  
36  
37 560 [30] Hodge, S. J., Bell, M. B. & Cant, M. A. 2011 Reproductive competition and the  
38 561 evolution of extreme birth synchrony in a cooperative mammal. *Biology Letters* **7**,  
39 562 54-56.  
40  
41  
42 563 [31] Neal, E. 1971. The banded mongoose, *Mungos mungo* Gmelin. *East African Wildlife*  
43 564 *Journal* **8**, 63-71.  
44  
45  
46 565 [32] Rood, J. P. 1975. Population dynamics and food habits of the banded mongoose. *East*  
47 566 *African Wildlife Journal* **13**, 89-111.  
48  
49  
50 567 [33] Koenig, W. D. & Dickinson, J. L. 2016 *Cooperative Breeding in Vertebrates: Studies of*  
51 568 *Ecology, Evolution, and Behavior*, Cambridge, Cambridge University Press.  
52  
53  
54 569 [34] Cant, M. A., Nichols, H. J., Thompson, F. J. & Vitikainen, E. 2016 Banded mongooses:  
55 570 demography, life history, and social behavior. *Cooperative Breeding in Vertebrates:*  
56 571 *Studies of Ecology, Evolution, and Behavior*, pp318-337, Cambridge, Cambridge  
57 572 University Press.  
58  
59  
60

- 1  
2  
3 573 [35] Thompson, F. J., Marshall, H. H., Vitikainen, E. I., Young, A. J., & Cant, M. A. (2017).  
4 574 Individual and demographic consequences of mass eviction in cooperative banded  
5 575 mongooses. *Animal Behaviour*, **134**, 103-112.  
6  
7  
8 576 [36] Cant, M. A., Vitikainen, E. & Nichols, H. J. 2013 Demography and social evolution of  
9 577 banded mongooses. *Advances in the Study of Behavior*, Vol. **45**, pp. 407-445.  
10 578 Academic Press.  
11  
12  
13  
14 579 [37] Gilchrist, J. S. 2004 Pup escorting in the communal breeding banded mongoose:  
15 580 behavior, benefits, and maintenance. *Behavioral Ecology* **15**, 952-960.  
16  
17  
18 581 [38] Cant, M. A. 2000 Social control of reproduction in banded mongooses. *Animal*  
19 582 *Behaviour* **59**, 147-158.  
20  
21  
22 583 [39] Nichols, H. J., Amos, W., Cant, M. A., Bell, M. B. V. & Hodge, S. J. 2010 Top males  
23 584 gain high reproductive success by guarding more successful females in a  
24 585 cooperatively breeding mongoose. *Animal Behaviour* **80**, 649-657.  
25  
26  
27  
28 586 [40] Thompson, F. J., Cant, M. A., Marshall, H. H., Vitikainen, E. I., Sanderson, J. L.,  
29 587 Nichols, H. J., Gilchrist, J. S., Bell, M. B., Young, A. J. & Hodge, S. J. 2017  
30 588 Explaining negative kin discrimination in a cooperative mammal society.  
31 589 *Proceedings of the National Academy of Sciences of the United States of America*,  
32 590 201612235.  
33  
34  
35  
36 591 [41] Thompson, F. J., Marshall, H. H., Sanderson, J. L., Vitikainen, E. I., Nichols, H. J.,  
37 592 Gilchrist, J. S., Young, A. J., Hodge, S. J. & Cant, M. A. 2016 Reproductive  
38 593 competition triggers mass eviction in cooperative banded mongooses. *Proceedings*  
39 594 *of the Royal Society of London B* 20152607.  
40  
41  
42  
43 595 [42] Cant, M. A., Hodge, S. J., Gilchrist, J. S., Bell, M. B. V. & Nichols, H. J. 2010  
44 596 Reproductive control via eviction (but not the threat of eviction) in banded  
45 597 mongooses. *Proceedings of the Royal Society of London B* **277**, 2219-2226.  
46  
47  
48  
49 598 [43] Inzani, E. L., Marshall, H. H., Sanderson, J. L., Nichols, H. J., Thompson, F. J.,  
50 599 Kalema-Zikusoka, G., Hodge, S. J., Cant, M. A. & Vitikainen, E. I. 2016 Female  
51 600 reproductive competition explains variation in prenatal investment in wild banded  
52 601 mongooses. *Scientific Reports* **6**, 20013.  
53  
54  
55  
56 602 [44] Gilchrist, J. S. 2006 Female eviction, abortion, and infanticide in banded mongooses  
57 603 (Mungos mungo): implications for social control of reproduction and synchronized  
58 604 parturition. *Behavioral Ecology* **17**, 664-669.

- 1  
2  
3 605 [45] Jordan, N. R., Mwanguhya, F., Kyabulima, S., Ruedi, P. & Cant, M. A. 2010 Scent  
4 606 marking within and between groups of wild banded mongooses. *Journal of Zoology*  
5 607 **280**, 72-83.  
6  
7  
8  
9 608 [46] Hadfield, J., Richardson, D. & Burke, T. 2006 Towards unbiased parentage  
10 609 assignment: combining genetic, behavioural and spatial data in a Bayesian  
11 610 framework. *Molecular Ecology* **15**, 3715-3730.  
12  
13  
14 611 [47] Jones, O. R. & Wang, J. 2010 COLONY: a program for parentage and sibship  
15 612 inference from multilocus genotype data. *Molecular Ecology Resources* **10**, 551-555.  
16  
17  
18 613 [48] Sanderson, J. L., Wang, J., Vitikainen, E. I., Cant, M. A. & Nichols, H. J. 2015 Banded  
19 614 mongooses avoid inbreeding when mating with members of the same natal group.  
20 615 *Molecular Ecology* **24**, 3738-3751.  
21  
22  
23  
24 616 [49] Wells, D. A., Cant, M. A., Nichols, H. J., & Hoffman, J. I. (2018). A high-quality pedigree  
25 617 and genetic markers both reveal inbreeding depression for quality but not survival in  
26 618 a cooperative mammal. *Molecular Ecology* **27**, 2271-2288.  
27  
28  
29  
30 619 [50] Gilchrist, J. S. 2008 Aggressive monopolization of mobile carers by young of a  
31 620 cooperative breeder. *Proceedings of the Royal Society B* **275**, 2491-2498.  
32  
33  
34 621 [51] Müller, C. A. & Manser, M. B. 2008 Mutual recognition of pups and providers in the  
35 622 cooperatively breeding banded mongoose. *Animal Behaviour* **75**, 1683-1692.  
36  
37  
38 623 [52] Gilchrist, J. S., Otali, E., Mwanguhya, F. 2008. Caregivers recognize and bias response  
39 624 towards individual young in a cooperative breeding mammal, the banded mongoose.  
40 625 *Journal of Zoology* **275**, 41-46.  
41  
42  
43 626 [53] Marshall, H. H., Sanderson, J. L., Mwanguhya, F., Businge, R., Kyabulima, S., Hares,  
44 627 M. C., Inzani, E., Kalema-Zikusoka, G., Mwesige, K., Thompson, F. J., Vitikainen, E.  
45 628 I. K & Cant, M. A. 2016. Variable ecological conditions promote male helping by  
46 629 changing banded mongoose group composition. *Behavioral Ecology* **27**, 978-987.  
47  
48  
49  
50 630 [54] Nichols, H. J., Amos, W., Bell, M. B. V., Mwanguhya, F., Kyabulima, S. & Cant, M. A.  
51 631 2012 Food availability shapes patterns of helping effort in a cooperative mongoose.  
52 632 *Animal Behaviour* **83**, 1377-1385.  
53  
54  
55  
56 633 [55] Freckleton, R. P. 2011 Dealing with collinearity in behavioural and ecological data:  
57 634 model averaging and the problems of measurement error. *Behavioral Ecology and*  
58 635 *Sociobiology* **65**, 91-101.  
59  
60

- 1  
2  
3 636 [56] Engqvist, L. 2005 The mistreatment of covariate interaction terms in linear model  
4 637 analyses of behavioural and evolutionary ecology studies. *Animal Behaviour* **70**.
- 5  
6  
7 638 [57] Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. 2006 Why do  
8 639 we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*  
9 640 **75**, 1182-1189.
- 10  
11  
12 641 [58] Team, R. C. 2014 R: A language and environment for statistical computing. Vienna,  
13 642 Austria: R Foundation for Statistical Computing; 2014.
- 14  
15  
16 643 [59] Bates D, Mächler M, Bolker B & Walker S 2015. Fitting linear mixed-effects models  
17 644 using lme4. *Journal of Statistical Software* **67**, 1-48.
- 18  
19  
20 645 [60] Forstmeier, W., & Schielzeth, H. 2011. Cryptic multiple hypotheses testing in linear  
21 646 models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and*  
22 647 *Sociobiology* **65**, 47-55.
- 23  
24  
25 648 [61] Garratt, M., Lemaître, J.F., Douhard, M., Bonenfant, C., Capron, G., Warnant, C., Klein,  
26 649 F., Brooks, R.C. and Gaillard, J.M. 2015. High juvenile mortality is associated with  
27 650 sex-specific adult survival and lifespan in wild roe deer. *Current Biology* **25**, 759-763.
- 28  
29  
30 651 [62] Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S.,  
31 652 Pearson, D., Plotsky, P. M. & Meaney, M. J. 1997 Maternal care, hippocampal  
32 653 glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress.  
33 654 *Science* **277**, 1659-1662.
- 34  
35  
36 655 [63] Cameron, N. M., Fish, E. W. & Meaney, M. J. 2008 Maternal influences on the sexual  
37 656 behavior and reproductive success of the female rat. *Hormones and Behavior* **54**,  
38 657 178-184.
- 39  
40  
41 658 [64] Champagne, F. A., Francis, D. D., Mar, A. & Meaney, M. J. 2003 Variations in maternal  
42 659 care in the rat as a mediating influence for the effects of environment on  
43 660 development. *Physiology and Behavior* **79**, 359-371.
- 44  
45  
46 661 [65] Croft, D. P., Brent, L. J., Franks, D. W. & Cant, M. A. 2015 The evolution of prolonged  
47 662 life after reproduction. *Trends in Ecology and Evolution* **30**, 407-416.
- 48  
49  
50 663 [66] Lahdenperä, M., Mar, K. U. & Lummaa, V. 2016 Nearby grandmother enhances calf  
51 664 survival and reproduction in Asian elephants. *Scientific Reports* **6**, 27213.
- 52  
53  
54  
55  
56  
57  
58  
59  
60



- 1  
2  
3 665 [67] Brent, L. J., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A. & Croft, D. P.  
4 666 2015 Ecological knowledge, leadership, and the evolution of menopause in killer  
5 667 whales. *Current Biology* **25**, 746-750.  
6  
7  
8 668 [68] Rogers, A. R. 1993 Why menopause? *Evolutionary Ecology* **7**, 406-426.  
9  
10  
11 669 [69] Hill, K. & Hurtado, A. M. 1996 *Ache Life History: the ecology and demography of a*  
12 670 *foraging people*. New York, de Gruyter.  
13  
14  
15 671 [70] Johnstone, R. A., Cant, M. A., & Field, J. 2012. Sex-biased dispersal, haplodiploidy and  
16 672 the evolution of helping in social insects. *Proceedings of the Royal Society of*  
17 673 *London B* **279**, 787-793.  
18  
19  
20  
21 674  
22 675

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676 **TABLES**

677 Table 1. Predictors of body mass (in grams) at sexual maturity (one year). Results from GLMMs with  
 678 litter and social group as random factors. For categorical fixed factors, parameter estimates show the  
 679 estimated difference between the level in [brackets] and the level represented by the intercept.  
 680 Nonsignificant interactions were dropped to allow significance testing of main terms, but models were  
 681 not simplified further. To improve model convergence, pup weight and rainfall were standardised by  
 682 subtracting the mean and dividing by the standard deviation.

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 Body mass (g) at maturity, at one years of age
 

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Fixed effects	$\beta \pm SE$	$\chi^2_1$	<i>P</i>
(intercept)	1102.57 $\pm$ 47.50		
Rainfall (std)	6.53 $\pm$ 12.04	0.304	0.581
Body mass at emergence (std)	52.66 $\pm$ 11.75	18.90	1.378 $\times$ 10 <sup>-5</sup>
Escorting index	89.04 $\pm$ 33.53	6.846	0.0089
Sex [male]	57.23 $\pm$ 18.58	9.439	0.0021
Sex $\times$ Escorting index <sup>§</sup>	42.32 $\pm$ 64.97	0.434	0.510
Number of observations	203 individuals, 82 litters, 11 packs		

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688 Table 2. Predictors of lifetime reproductive success in individuals that reached maturity  
 689 (lifespan >365 days). Results from GLMMs with litter and social group as random factors.

(A) Predictors of lifetime reproductive success: model without offset

	<i>Females</i>			<i>Males</i>		
Fixed effects	$\beta \pm SE$	$\chi^2_1$	<i>P</i>	$\beta \pm SE$	$\chi^2_1$	<i>P</i>
(intercept)	-0.695 $\pm$ 0.414			-1.276 $\pm$ 0.592		
Rainfall (std)	0.506 $\pm$ 0.237	4.905	0.027	-0.349 $\pm$ 0.350	0.976	0.323
Mass at emergence (std)	-0.461 $\pm$ 0.189	5.685	0.017	0.115 $\pm$ 0.235	0.238	0.626
Escorting index	1.691 $\pm$ 0.506	12.388	0.0004	-0.392 $\pm$ 0.560	0.491	0.483
Mass at one year (std)	0.476 $\pm$ 0.197	4.321	0.038	0.746 $\pm$ 0.233	11.027	0.0009
Number of observations	76 individuals, 55 litters, 8 groups			109 individuals, 61 litters, 9 groups		

(B) Predictors of lifetime reproductive success: model using lifespan as an offset

	<i>Females</i>			<i>Males</i>		
Fixed effects	$\beta \pm SE$	$\chi^2_1$	<i>P</i>	$\beta \pm SE$	$\chi^2_1$	<i>P</i>
(intercept)	-1.094 $\pm$ 0.346			-1.989 $\pm$ 0.481		
Rainfall (std)	0.310 $\pm$ 0.185	2.972	0.085	-0.342 $\pm$ 0.269	1.588	0.208
Mass at emergence (std)	-0.343 $\pm$ 0.160	2.596	0.107	-0.219 $\pm$ 0.218	1.016	0.313
Escorting index	0.859 $\pm$ 0.436	4.122	0.042	-0.276 $\pm$ 0.552	0.251	0.617
Mass at one year (std)	0.533 $\pm$ 0.152	4.934	0.026	0.508 $\pm$ 0.216	5.523	0.019
Number of observations	76 Individuals, 55 litters, 8 groups			109 Individuals, 61 litters, 9 groups		

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3 693 **FIGURE LEGENDS**  
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6 695 Figure 1. Escorting and body mass at sexual maturity (one year). For both females and  
7 696 males, pups that were more closely escorted by adult helpers from days 30 to 90 of  
8 697 development were heavier at sexual maturity (1 year). Body mass at maturity is a positive  
9 698 predictor of lifetime reproductive success in both sexes. Panel A. Females; B. Males. Model  
10 699 prediction  $\pm$  SE from a GLMM with litter and social group as random terms. Data from 203  
11 700 individuals from 82 litters in 11 groups.  
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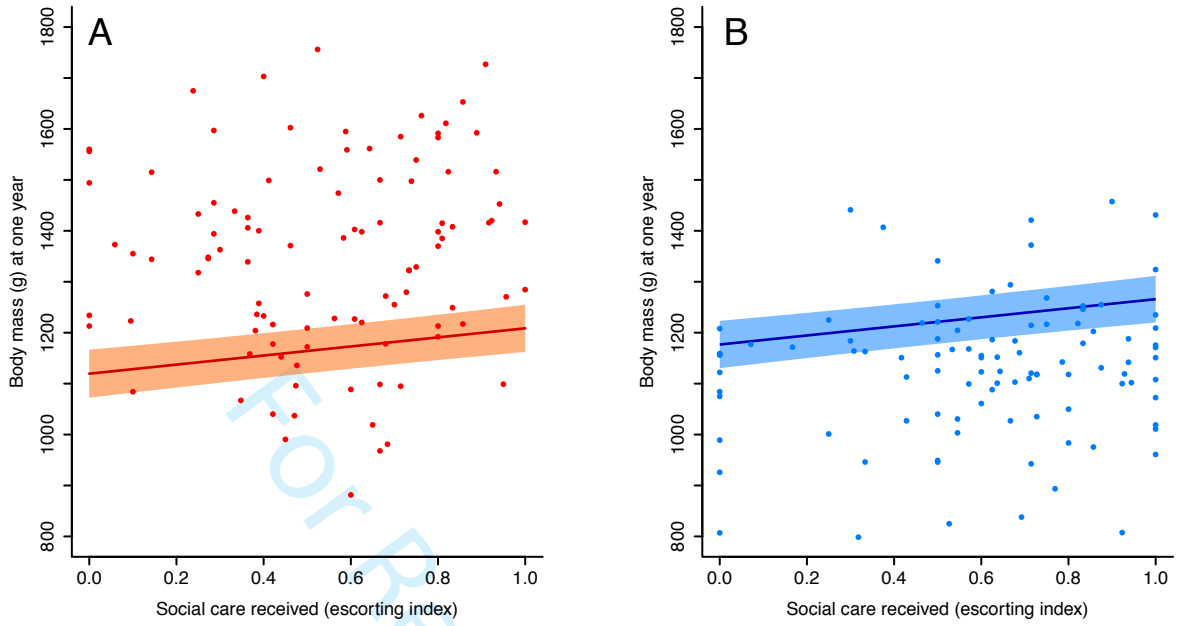
17 701

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19 702 Figure 2. Escorting and lifetime reproductive success. A. In females, increased escorting  
20 703 was associated with higher lifetime reproductive success as adults, independent of the  
21 704 positive effect of escorting on adult body mass. B. In males, there was no additional effect  
22 705 of escorting *per se*, controlling for effects on body mass. Model prediction  $\pm$  SE from a  
23 706 GLMM with litter and social group as random terms. Data from 76 individuals from 55  
24 707 communal litters in 8 groups.  
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