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### Article

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1 **Biased escorts: offspring sex, not relatedness explains alloparental care patterns in a**  
2 **cooperative breeder**

3

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17

18 ABSTRACT

19

20 Kin selection theory predicts that animals should direct costly care where inclusive fitness  
21 gains are highest. Individuals may achieve this by directing care at closer relatives, yet  
22 evidence for such discrimination in vertebrates is equivocal. We investigated patterns of  
23 cooperative care in banded mongooses, where communal litters are raised by adult 'escorts'  
24 who form exclusive caring relationships with individual pups. We found no evidence that  
25 escorts and pups assort by parentage or relatedness. However, the time males spent  
26 escorting increased with increasing relatedness to the other group members, and to the pup  
27 they had paired with. Thus we found no effect of relatedness in partner choice, but (in  
28 males) increasing helping effort with relatedness once partner choices had been made.  
29 Unexpectedly, the results showed clear assortment by sex, with female carers being more  
30 likely to tend to female pups, and male carers to male pups. This sex-specific assortment in  
31 helping behaviour has potential lifelong impacts on individual development, and may impact  
32 the future size and composition of natal groups and dispersing cohorts. Where relatedness  
33 between helpers and recipients is already high, individuals may be better off choosing  
34 partners using predictors of the costs and benefits of cooperation, without the need for  
35 possibly costly within-group kin discrimination.

36

37 Keywords: Cooperative breeding, nepotism, helping, altruism, sex-biased care, alloparental  
38 care

39

## 40 INTRODUCTION

41

42 Hamilton's rule [1] predicts when costly helping behaviour can evolve and provides a simple  
43 yet very broad framework for understanding evolution of altruism. Hamilton's rule predicts  
44 that, other things being equal, costly care should be directed to closer relatives. When  
45 relatedness to the potential recipients of helping behaviour varies, actors may be able to  
46 discriminate and direct help using cues that correlate with genetic relatedness [2]. Studies  
47 on cooperatively breeding animals have found evidence that choice of recipient or helping  
48 effort is positively correlated with kinship (e.g. white-fronted bee-eaters, [3]; Seychelles  
49 warblers [4] and long-tailed tits, [5]), or, in a rare example, negatively correlated with  
50 kinship [6]. These studies support the notion that the capacity for kin discrimination is  
51 widespread among cooperatively breeding vertebrates.

52 In many contexts, however, kin discrimination is notably absent. In social insects, for  
53 example, individuals discriminate between nestmates and non-nestmates, but typically do  
54 not discriminate degrees of relatedness among nestmates [7-9]. In many biparental and  
55 cooperative breeding systems, male parental investment is not related to paternity share  
56 (e.g. [10-12]). A lack of kin discrimination in these contexts may reflect limitations imposed  
57 by the use of shared environmental or social cues of relatedness or parentage, or the costs  
58 of distinguishing degrees of relatedness when most interactions occur among kin of some  
59 kind [7]. However, it may also reflect selection on recipients to conceal identity. For example,  
60 being identified as highly related to a potential helper might simultaneously expose an  
61 individual to harmful or spiteful actions from non-related individuals [13]. Actors may thus  
62 be unable to discriminate even if it were in their interest to do so, if the benefits from

63 directed care are outweighed by the costs of the recipient being discriminated against by  
64 other group members [14].

65 Hamilton's rule also predicts that helpers should be sensitive to variation in the  
66 benefits that different recipients stand to gain from a helpful act, and variation in personal  
67 fitness costs of allocating help to one individual over another. In mixed sex groups, these  
68 costs and benefits are likely to vary according to the sex of both actors and recipients. For  
69 example, helping may entail greater energetic costs, or greater risks, for one sex than  
70 another because of sex asymmetries in size, or physiological specialisation (e.g.  
71 allousuckling; [15-16]). In males, helping may be incompatible with guarding fertile females, so  
72 they may experience greater opportunity costs by investing in care rather than in  
73 reproductive competition [17]. From the perspective of recipients, the benefit conferred by  
74 help may also vary systematically with sex. For example, in sexually dimorphic mammals  
75 offspring of the larger sex have higher energy requirements and may gain more (in terms of  
76 future reproductive success) from alloparental investment received (e.g. [18-20]).

77 Here we ask whether variation in relatedness, or in ecological and social correlates  
78 of costs and benefits of helping, predict patterns of alloparental care in cooperatively  
79 breeding banded mongooses (*Mungos mungo*). This species is ideal to test the factors that  
80 influence targeting of care because there are numerous helpers of each sex and numerous  
81 potential recipients of varying relatedness. Multiple females breed in each breeding  
82 attempt, and give birth to a synchronous, communal litter, typically on the same day [21-23].  
83 After these pups emerge from the den (at about 1 month of age) they are cared for by adult  
84 'escorts' who form exclusive one-to-one helping relationships with particular pups, feeding  
85 and protecting them, and passing on foraging skills [24-25]. Both pups and adults exercise  
86 influence over the formation of escorting relationships: pups compete for certain escorts

87 [26], and escorts recognise and single out their 'own' pup for preferential care [24,26,27].

88 While some pups in the litter are escorted by a particular escort every day, other pups

89 receive much less care, and must fend for themselves from an early age. Escorted pups

90 receive more food, grow faster, and are more likely to survive to independence than non-

91 escorted pups [28].

92 We used a 15-year dataset on escorting in wild banded mongooses to test the

93 relative influence of sex and relatedness on patterns of helping behaviour within and

94 between litters. Specifically we investigated the following three questions:

95 (1) Do patterns of relatedness predict allocation of care across litters?

96 (2) Does relatedness and/or sex predict which helpers and offspring form escorting

97 associations, or the strength of these associations?

98 (3) What predicts variation in the total amount of escorting received by the offspring?

99

100 As we demonstrate, kinship has differing effects on helping effort and assortment, and our

101 study reveals strong patterns of sex-specific helping. Our results also support earlier claims

102 that mothers cannot recognise their own young in this communal breeding system.

## 103 MATERIAL AND METHODS

104

105

106 **Study species & population**

107

108 Banded mongooses (*Mungos mungo*) are cooperatively breeding, diurnal carnivores in the  
109 family Herpestidae that are common in central and eastern parts of Africa. We conducted  
110 the study on a population of wild banded mongooses living on and around the Mweya  
111 peninsula of Queen Elizabeth National Park, Uganda (0 12' S, 27 54'E). For details of the field  
112 site and the population, see [29] and references therein. Reproduction is synchronised  
113 within social groups, and females give birth up to four times per year. The resulting mixed  
114 litter is reared communally by group members; both parents and nonbreeding group  
115 members contribute to pup care [30].

116 All mongooses in our study population are individually marked using either unique  
117 hair-shave patterns or colour-coded collars, and most animals are habituated to close  
118 observation from at least 5m and trained to step onto portable electronic scales to obtain  
119 weight measurements. One to two mongooses in each group are fitted with a radio collar  
120 weighing 26 to 30 g (Sirtrack Ltd, Havelock North, New Zealand) to allow the groups to be  
121 located. Pups were first captured at emergence from the den, at around 3-4 weeks of age,  
122 weighed, sexed, and marked with permanent hair dye (see [31] for further details of the  
123 trapping procedure). When individuals were first trapped, a 2-mm skin sample was taken for  
124 extraction of DNA, which was used to construct a pedigree for assigning parentage and  
125 calculation of pairwise relatedness values. The final pedigree used both Masterbayes 2.51  
126 [32] and COLONY 2.0.5.7 [33] to infer parentage; 95 % of parental assignments of individuals

127 included in this study were made with > 90 % confidence. For full details of DNA extraction,  
128 genotyping, parentage assignment and pedigree construction see [34]. Weather data  
129 (rainfall) were collected by the Mweya weather station, and cumulative rainfall during the 30  
130 days before the communal litter was born was used as a proxy of resource availability, as this  
131 has been found to affect competition and patterns of care in banded mongooses (e.g. [35-  
132 37]).

133

134

### 135 **Quantifying escorting behaviour**

136

137 Banded mongooses exhibit a conspicuous form of alloparental care termed ‘escorting’,  
138 whereby older individuals form one-on-one helping relationships with pups ([38] and  
139 references therein). Escorts stay close to their associated pup, feeding, carrying, grooming,  
140 and protecting it from predators [24], Fig. 1). Escorting starts when pups first emerge from  
141 the den at around 4 weeks old, and continues until pups reach nutritional independence at  
142 the age of 3 months (the ‘escorting period’). We observed escorting behaviour in 143  
143 communal litters in 12 social groups (mean group size 22 adult individuals; SD 7.3, range 7-  
144 37) that inhabited the study area between the years 2000-2015. During this escorting  
145 period, groups were visited on average 12 times for a minimum of 20 minutes (the duration  
146 of one focal observation session). Relatedness estimates and pup and escort weights were  
147 available for most but not all litters, so the actual sample size varied according to the  
148 available data and set of predictor variables included in each analysis, see details below and  
149 Supplementary Information Tables S1-S3.



150 An adult individual was termed an escort if it associated closely with the focal pup  
151 i.e. spent more than half of the 20-minute observation session within 0.5m of the focal pup  
152 (Fig. 1). Detailed focal observations of escorting effort of care show that pup provisioning  
153 rates are correlated with time spent in close association ( $r = 0.56$ ,  $n = 129$ ,  $P < 0.001$  [39]),  
154 and escorts preferentially carry, groom and play with the pups they associate with  
155 [24,27,39]). Therefore, proportion of the sessions during which an adult was observed  
156 escorting a pup was used as a measure of its escorting effort, and the proportion of the  
157 observation sessions a pup was seen being escorted by an adult was used as a measure of  
158 escorting it received. Data on parentage and relatedness were not available at the time of  
159 behavioral data collection, and hence all the observations and scoring of escorting behavior  
160 were done blind as to the relatedness and parentage between pup and its escort.

161

## 162 **Ethics**

163

164 All research was carried out under permit from Uganda Wildlife Authority (UWA) and  
165 Uganda National Council for Science and Technology (UNCST). All procedures adhered to the  
166 Guidelines for the Treatment of Animals in Behavioural Research and Teaching, published by  
167 the Association for the Study of Animal Behaviour, and received prior approval from UWA,  
168 UNCST, and the Ethical Review Board of the University of Exeter.

169

170

**171 Statistical analyses and model selection**

172

173 We included as potential escorts all individuals that were present in a social group and over  
174 6 months old at the time the litter was born, and escorting relationships between adults and  
175 pups, and the escorting effort given and received in those relationships were defined as  
176 above. We used Generalised Linear Mixed Models (GLMMs) with binomial error structure  
177 and logit link function, and social group, litter, and individual identity were included as  
178 random effects to control for repeated sampling as detailed in the analysis sections below.

179 Statistical analyses were done in R, version 3.3.0 [40] and GLMM models fitted using R  
180 package lme4 [41]. Significance of terms was determined using likelihood ratio tests [41],  
181 and non-significant interactions were dropped from final models to allow significance testing  
182 of the main terms [42]. As female reproductive conflict increases with increasing numbers of  
183 females in the group (e.g. [22, 43]) and male reproductive success similarly diminishes as a  
184 function of number of males in the group [44], we included the number of same-sex  
185 individuals in the group as proxy of the intensity of reproductive competition, but did not  
186 include total group size as this was highly collinear with both (number of females:  $R^2 = 0.68$ ,  
187 number of males:  $R^2 = 0.95$ ). Because males and females are known to differ in determinants  
188 of their helping effort (see eg. [17,35]), we carried out analyses 1 and 2 separately for males  
189 and females. Despite relatedness to the litter being correlated with parentage ( $r^2 = 0.56$ ), we  
190 included both in the models as it did not affect our results; for a more detailed discussion  
191 see the Supplementary Information. The level of correlation between other predictor  
192 variables in our models was below the level identified by Freckleton [45] as problematic for  
193 estimating linear models (all  $r < 0.4$ ). The full analysis results including non-significant  
194 parameter estimates are presented in the Supplementary Tables S1-S3.

195

196 We also used t-test to look at overall sex differences in pup weight, and Wilcoxon

197 signed rank tests to compare the total escorting effort female and male pups received.

198 Average relatedness among realised and potential pup-escort pairs was compared using a t-

199 test with 10000 permutations, implemented in the R-package broman [46].

200

201

202 **Question 1: Do patterns in relatedness predict allocation of care across litters?**

203

204 First, we tested whether characteristics of the litter, social group, or those of the potential

205 escort at the time the litter was born, predicted the escorting behavior of adults in the

206 group. Because different factors may predict whether an individual helps at all, and their

207 total effort when they help, this analysis was conducted in two parts. First, we treated escort

208 status as a binomial variable whether or not individual was observed escorting in that litter

209 at all. Second, we fitted the number of sessions an individual was observed escorting as the

210 binomial response variable with the total number of observation sessions as the

211 denominator, for individuals that had been escorting at least once in that litter. Splitting the

212 analyses in this way also accounted for problems with zero-inflation in the data. Predictor

213 variables in both analyses were rainfall during the previous month, weight and age of the

214 potential escort and their interaction, number of pups in the litter, number of same-sex

215 adults in the group, parentage (whether or not the focal individual was parent to any pups in

216 that litter), the focal individual's average relatedness to pups in the litter, and the focal

217 individual's average relatedness to adults in the group. Both analyses included individual,

218 litter and social group as random effects.

219

220

221 **Question 2: Does relatedness and/or sex predict which helpers and pups form escorting**  
222 **associations, or the strength of these associations?**

223

224 We then looked at pairwise interactions between pups and escorts within-litter. Similar to  
225 analysis 1, this analysis was done in two parts, as different factors may predict which pups  
226 an adult associates with, and how much care is given when they do. First, we conducted a  
227 binomial GLMM looking at whether an escort associated with a given pup (0/1). For this all  
228 potential pairs of pups and escorts were constructed, so that all individuals that were  
229 observed escorting at least once in a given litter were included as potential escorts for all the  
230 pups in that litter. Predictor variables were sex of the pup, pup weight, parentage, and  
231 relatedness between the adult and the pup, and to investigate whether escorting might be  
232 contingent on within-sex competition, we also included as a predictor the interaction  
233 between the number of same-sex adults and the sex of the pup. Second, among observed  
234 pup-escort pairs, we used a binomial GLMM with the proportion of observation sessions the  
235 focal pup was being escorted by the focal adult as the binomial response variable, using the  
236 same set of predictor variables as above. While most of the relationships are dyadic in  
237 nature, an adult can sometimes escort multiple pups in a litter and a pup may have multiple  
238 escorts. To account for this, we included both pup and escort identity, as well as litter and  
239 social group, as random effects in these analyses.

240

241 **Question 3. What predicts variation in the total amount of care received by the offspring?**

242

243 Finally, we looked at escorting relationships from the pup perspective, with the analysis split  
244 as above. First, we looked at whether or not a pup associated with any escort (0/1), with pup  
245 sex, weight, litter size and their two-way interactions as predictors, and litter and social  
246 group as random effects (not individual, as each pup was only included once in this dataset).  
247 Second, we looked at predictors of the amount of care those pups received that had an  
248 escort (proportion of observation sessions they were escorted) with pup weight, pup sex,  
249 litter size, sex of the escort, parentage, and relatedness between pup and the escort as  
250 covariates. In cases where the pup had multiple escorts, we included the characteristics of  
251 the adult that provided most care. In this analysis escort identity, litter, and social group  
252 were included as random effects.  
253  
254

255 **RESULTS**

256

257 **Question 1:** Do patterns in relatedness predict allocation of care across litters?

258

259 Neither relatedness to the litter (after controlling for the effect of parentage; see  
 260 Supplementary Information) nor relatedness to other group members predicted the  
 261 probability that a female escorted in a given litter (Relatedness to the litter:  $\chi^2_1 = 2.25$ ,  $P =$   
 262  $0.133$ ; relatedness to the group:  $\chi^2_1 = 0.43$ ,  $P = 0.511$ ). Females were more likely to escort  
 263 when they had mothered pups in the current litter ( $\beta \pm SE: 0.98 \pm 0.30$ ,  $\chi^2_1 = 11.00$ ,  $p <$   
 264  $0.001$ ). In addition, the probability that each female would escort in the current litter  
 265 declined with the number of adult females in the group ( $\beta \pm SE: -0.31 \pm 0.06$ ,  $\chi^2_1 = 23.8$ ,  $P <$   
 266  $0.001$ , Fig. 2A), and increased with increasing litter size (litter size:  $\beta \pm SE = 0.14 \pm 0.04$ ,  $\chi^2_1 =$   
 267  $15.94$ ,  $P < 0.001$ ). The effect of weight on escorting probability was contingent on age, with  
 268 the probability of escorting declining with age in heavier but not in lighter females  
 269 (interaction weight x age:  $\chi^2_1 = 5.10$ ,  $P = 0.024$ ; Supplementary Table S1A and Fig. S1A).

270 Among those females that escorted, the total individual escorting effort per litter  
 271 (proportion of sessions seen escorting) decreased as the number of females in the group  
 272 increased ( $\beta \pm SE = -0.068 \pm 0.03$ ,  $\chi^2_1 = 4.49$ ,  $P = 0.024$ ), but other terms had no effect on the  
 273 total amount of help escorting females allocated to a litter; see Supplementary Table S1 for  
 274 full results.

275

276 For males, neither parentage nor relatedness predicted the probability that a male  
 277 escorted in a given litter (parentage:  $\chi^2_1 = 0.107$ ,  $P = 0.744$ ; relatedness to litter:  $\chi^2_1 = 0.24$ ,  $P$   
 278  $= 0.826$ ; relatedness to adults:  $\chi^2_1 = 0.08$ ,  $P = 0.775$ ). Like females, the probability of a male  
 279 escorting in a given litter declined with increasing number of adult males in the group ( $\beta \pm$

280 SE:  $= -0.15 \pm 0.03$ ,  $\chi^2_1 = 16.99$ ,  $P < 0.001$ , Fig. 2B) and increased with increasing litter size ( $\beta$   
 281  $\pm$  SE  $= 0.21 \pm 0.034$ ,  $\chi^2_1 = 35.05$ ,  $P < 0.001$ ). The probability of escorting also increased with  
 282 increasing rainfall ( $\beta \pm$  SE  $= 0.27 \pm 0.13$ ,  $\chi^2_1 = 3.95$ ,  $P = 0.047$ ). Among those males that did  
 283 escort, total escorting effort (proportion of sessions seen escorting) increased with  
 284 relatedness to other adults in the group ( $\beta \pm$  SE  $= 1.80 \pm 0.65$ ,  $\chi^2_1 = 7.67$ ,  $P = 0.006$ ; Fig. S2),  
 285 but not with relatedness to the litter ( $\chi^2_1 = 0.11$ ,  $P = 0.74$ ). The escorting effort of males also  
 286 declined with increasing number of adult males in the group ( $\beta \pm$  SE  $= -0.036 \pm 0.01$ ,  $\chi^2_1 =$   
 287  $13.9$ ,  $P < 0.001$ ) but litter size had no effect on the total escorting effort ( $\chi^2_1 = 0.22$ ,  $P = 0.637$ ).  
 288 As in females, the effect of weight on escorting depended on age, with both the likelihood of  
 289 escorting and escorting effort decreasing with age in heavy but not in light individuals (SI  
 290 Table S1, Fig. S1B). The escorting effort of males was not predicted by rainfall ( $\chi^2_1 = 0.17 \pm$   
 291  $0.677$ ).

292

293 **Question 2:** Does relatedness and/or sex predict which helpers and offspring form escorting  
 294 associations, or the strength of these associations?

295

296 Pairwise relatedness did not predict associations in female escorts ( $\chi^2_1 = 0.031$ ,  $P = 0.859$ )  
 297 nor in male escorts ( $\chi^2_1 = 0.76$ ,  $P = 0.383$ ), and neither did parentage (females:  $\chi^2_1 = 0.66$ ,  $p$   
 298  $= 0.414$ ; males:  $\chi^2_1 = 0.05$ ,  $P = 0.832$ ). Average relatedness between realised pup-escort pairs  
 299 did not differ from that between pups and all potential escorts (average  $\pm$  SD: realized pairs:  
 300  $R = 0.211 \pm 0.169$ , all potential pairs:  $R = 0.208 \pm 0.171$ , permutation test:  $t = 0.172$ ,  $P =$   
 301  $0.87$ ). Parentage did not predict the amount of care escorts gave to a particular pup (female  
 302 escorts:  $\chi^2_1 = 0.18$ ,  $P = 0.675$ ; male escorts:  $\chi^2_1 = 0.01$ ,  $P = 0.934$ ). For males but not females,

303 escorting effort in escort-pup pairs increased with increasing dyadic relatedness between  
 304 escort and pup ( $\beta \pm SE = 0.83 \pm 0.32$ ,  $\chi^2_1 = 6.61$ ,  $P = 0.010$ , females:  $\chi^2_1 = 0.51$ ,  $P = 0.476$ ).

305

306 Both the sex of the escort and the pup predicted patterns of dyadic association (Fig. 3A).

307 Female escorts were more likely to pair with a female pup (59% of female escorts paired

308 with a female pup vs. 41% with a male pup; pup sex[M]:  $\beta \pm SE = -0.43 \pm 0.19$ ,  $\chi^2_1 = 4.94$ ,  $P =$

309 0.023, Fig. 3A) and allocated more care to female pups when there were fewer females in

310 the groups ( $\chi^2_1 = 8.85$ ,  $P = 0.003$ , Fig. 3B). Other factors did not predict dyadic association or

311 the amount of care provided by females, see table S2 for full results. Similarly, males were

312 more likely to associate with male pups (61% of male escorts paired with male pups vs. 39%

313 with female pups; pup sex[M]:  $\beta \pm SE = 0.40 \pm 0.12$ ,  $\chi^2_1 = 11.3$ ,  $P < 0.001$ , Fig. 3A), but

314 provided less care when there were more males in the group irrespective of the sex of the

315 pup ( $\beta \pm SE = +0.033 \pm 0.01$ ,  $\chi^2_1 = 8.8$ ,  $P = 0.003$ ; for full results see Supplementary table S2).

316

317 **Question 3:** What predicts variation in the total amount of care received by the offspring?

318

319 Compared to female pups, male pups received more care from helpers (proportion of

320 observation sessions being escorted for all escorted and non-escorted pups: mean  $\pm$  SE:

321 males  $0.478 \pm 0.017$  vs females  $0.425 \pm 0.019$ , Wilcoxon rank-sign test:  $N = 726$ ,  $W = 100150$ ,

322  $p = 0.034$ ). Male pups were also slightly heavier at emergence than females ( $204.7 \pm 3.1g$  vs.

323  $195.7 \pm 3.1g$ ,  $t_{724} = 2.07$ ,  $P = 0.039$ ).

324

325 The effect of pup weight on its probability of being escorted depended on sex of the pup:

326 larger pups more likely to be escorted, and the probability of escorting increased more



327 steeply with weight in female pups (weight x pup sex:  $\chi^2_1 = 6.43$ ,  $P = 0.042$ , Fig. 3C). When  
328 escorted, larger pups also received more care ( $\beta \pm SE = 0.063 \pm 0.031$ ,  $\chi^2_1 = 4.05$ ,  $P = 0.044$ )  
329 as did male pups ( $\beta \pm SE = 0.112 \pm 0.057$ ,  $\chi^2_1 = 3.80$ ,  $P = 0.051$ ; Fig. 3D). Pups in larger litters  
330 were no more or less likely to be escorted ( $\chi^2_1 = 0.01$ ,  $P = 0.907$ ) but received less care when  
331 escorted ( $\beta \pm SE = -0.024 \pm 0.01$ ,  $\chi^2_1 = 6.67$ ,  $P = 0.009$ ). Neither the relatedness between the  
332 pup and the escort providing most care, parentage, nor sex of the escort predicted the total  
333 amount of care that the escorted pups received (relatedness:  $\chi^2_1 = 0.46$ ,  $P = 0.496$ ; escort  
334 sex:  $\chi^2_1 = 1.74$ ,  $P = 0.187$ , parentage:  $\chi^2_1 = 0.08$ ,  $P = 0.775$ ).

335 **DISCUSSION**

336

337

338 Much research has focused on the influence of relatedness on selection for helping behavior

339 [47], but why individuals might conceal identity or avoid discrimination within groups is a

340 much less explored topic, particularly in vertebrates. The naive prediction from Hamilton's

341 rule is that care should be directed at closer relatives, but this ignores the problems that

342 being able to discriminate creates, both at the individual and at the group level. Nepotism

343 can be disruptive to the group and lead to selection against the very recognition cues that

344 form the basis of such discrimination [e.g. 7]. More pressingly, for the recipient to identify

345 themselves as highly related to some group members also comes at the cost of revealing

346 themselves as less related to others, exposing them to negative discrimination and spite

347 (e.g. [14, 48]). Where the average relatedness between helpers and helpes is high anyway,

348 such costs may override any benefit, making returns from discrimination marginal at best

349 [7,12]. In the banded mongoose, the average relatedness between potential helpers and

350 recipients was close to that between half-siblings ( $R \pm SD: 0.21 \pm 0.17$ ). In such systems

351 individuals may be better off adjusting their behaviour according to other predictors of costs

352 and benefits of cooperation, without the need for possibly costly within-group kin

353 discrimination, and this is indeed what we find in the banded mongoose.

354

355 In the banded mongoose, a striking feature of their cooperative behaviour is

356 the formation of one-to-one caring relationships termed 'escorting' [24]. Earlier studies

357 have suggested that pups have an active role in establishing relationships with particular

358 escorts [e.g. 26,27,49], implying that the escort-pup relationship is not solely the result of

359 choices made by the helper. However, previously we have been unable to exclude the

360 possibility that escorts were typically the parents of the pups they care for, bringing into  
361 question whether adults that engage in this behaviour should be termed helpers at all [50].  
362 This study shows that escorts do indeed care for pups that are not their own offspring, and  
363 that, despite the presence of high relatedness offspring within the communal litter, neither  
364 males nor females preferentially form pairwise associations with pups that are more related  
365 to them. Although females are more likely to escort when the current litter contains some of  
366 their own young, they do not preferentially pair with their own offspring, supporting  
367 previous claims that mothers do not or cannot discriminate their own young in the  
368 communal litter [51,21,38]. Moreover, neither pairwise relatedness nor parentage predicts  
369 the amount of care females allocated to an individual pup. The lack of kin discrimination by  
370 females is perhaps surprising given that escorting boosts the survival and growth of pups  
371 (e.g. [26,28]). However, in banded mongooses, the potential costs of nepotistic  
372 discrimination may be particularly high because within-group infanticide is common [52].  
373 Any pup advertising its close relatedness to a particular female (or, potentially, male) could  
374 be targeted by others, and could also lose out on allosuckling by other females, even if not  
375 directly aggressed [53].

376

377         In males, neither paternity nor relatedness to the pups predicted patterns of  
378 assortment in escort-pup relationships. Nor did relatedness predict male escorting effort  
379 across litters. However, we did find two correlations between relatedness and patterns of  
380 male helping. First, across litters, males increased the time spent escorting when they were  
381 more closely related on average to the rest of the group. Second, within pup-escort pairs,  
382 more related dyads spent more time together. These results might suggest kin discrimination  
383 by males. However, these patterns could also arise as a result of other factors that are

384 correlated with relatedness. For example, there may be subtle similarities in genetically  
385 heritable foraging preferences or character traits, such as preference of closed versus open  
386 habitat, or boldness and shyness, that could explain why more related partners spend more  
387 time together. There may also be subtle effects of group size on the observed relationships  
388 between escorts and pups. In small groups, in which relatedness is high, pups are  
389 particularly valuable in terms of group recruitment, and all adults may be more attentive  
390 escorts. Without cross-fostering experiments to manipulate which pups pair with which  
391 escorts, or experimental manipulation of group size, we are currently unable to fully  
392 understand the causality of the relationship between relatedness and helping effort in  
393 males.

394

395         We did find strong discrimination based on sex of the recipient. Both males and  
396 females were more likely to pair with a pup of their own sex, and reduced their overall  
397 helping effort in response to increasing number of same-sex adults in the group. As group  
398 size was highly correlated with both numbers of adult males and females, individuals may  
399 simply reduce their contribution to care as there are more helpers present. However,  
400 females also provided more care to female pups when adult female numbers were low,  
401 which implies that within-sex cooperation and competition may be driving the preferential  
402 direction of help to the same sex. For female banded mongooses there appears to be an  
403 optimal group size which maximises their reproductive success [52]. Females are evicted in  
404 same-sex cohorts when the number of breeding females grows large [53, 54, 55], and  
405 patterns of dispersal and eviction may therefore create incentives for female adults to adjust  
406 care given toward female pups depending on the competitive environment. Males may also  
407 have an incentive to target care toward other males, since males may be particularly

408 important in defending the territory against neighbouring groups and evicted cohorts of  
409 males that attempt to take over and supplant existing males [29].

410

411         Sex bias in care has been observed in many biparental birds as well as other  
412 cooperatively breeding mammals, with varying direction of bias and consequences for the  
413 offspring. For example, in the toc-toc (*Foudia sechellarum*) the brood is divided by sex post-  
414 fledging between the mother and the father [56] with no overall differences between the  
415 sexes in the amount of care. In zebra finches mothers preferentially provision sons over  
416 daughters, whilst fathers show no bias, and sons receive more food than daughters overall  
417 [57]. In social animals in particular, offspring of the same sex may be reproductive  
418 competitors or future helpers/soldiers, and depending on the system helpers might prefer to  
419 raise offspring of the same or different sex. For example, in the cooperatively breeding  
420 arabian babblers (*Turdoides squamiceps*) helpers invest in offspring of the opposite sex in  
421 order to avoid competition [58], as do spotted hyaenas (*Crocuta crocuta*), where males  
422 associate more with daughters, than with sons: [59]. Preferential helping of the same sex  
423 has been previously observed in the cooperatively breeding meerkat (*Suricatta suricata*).  
424 Similar to the banded mongoose, meerkat female helpers preferentially feed female pups,  
425 but males show no bias [60]. Females also provide more help than males. These patterns of  
426 care may be explained by sex differences in dispersal and the benefits of philopatry. In  
427 meerkats, males are the dispersing sex, and hence benefit less from any group  
428 augmentation benefits of helping compared to females. This explanation fits with our  
429 findings in the banded mongoose, where where both sexes remain in their natal group, and  
430 are also more likely to pair up with a pup of the same sex.

431

432 Another explanation for the sex bias in caring relationships observed here is that the  
433 competitive ability of the pups may be driving the association. Male banded mongooses are  
434 more likely to be escorts than females, and they also provide more care. Larger pups were  
435 more likely to be escorted, and received more care, despite the caring effort of individual  
436 helpers not being correlated with pup size. As male pups were on average slightly larger  
437 than female pups they also received more care overall, with the total amount of escorting  
438 care received increasing more steeply with size in female than in male pups. This result  
439 suggests that bigger pups may be able to secure the best helpers, which often are young  
440 males. Our results are consistent with previous findings that escort-pup associations may  
441 arise from competitive differences between pups [24,26]. They also highlight our recent  
442 findings that mothers invest in larger fetuses when postnatal reproductive competition is  
443 likely to be intense [43]. Priming offspring early in development to compete for escorts may  
444 be a good competitive strategy when there is little or no opportunity to discriminate and  
445 direct nepotism towards one's own offspring after birth.

446

447 To conclude, we find that partner choice in the banded mongoose escorting system  
448 are the result of sex-specific association but not fine-grained discrimination of dyadic  
449 relatedness. In this system, advertisement of relatedness or identity is likely to involve costs  
450 in terms of exposure to aggression or infanticide, which far outweigh any potential benefits  
451 of nepotistic assortment. By contrast, the sex of offspring is a conspicuous and unchanging  
452 trait, which may act as predictor of direct fitness returns of investment for male versus  
453 female helpers. Since escorts boost offspring survival [28], and pass on foraging traditions to  
454 the pups in their care [25], sex-biased patterns of assortment may have lasting impacts on  
455 sex-specific behaviour, group composition, and dispersal and breeding success of same sex

456 cohorts. Recent demographic models of social evolution have highlighted the impact of  
457 demography on selection for helping and harming (reviewed in [61]). Our findings raise the  
458 possibility that within-group assortative patterns of helping and harming can in turn feed up  
459 to influence demography in natural populations.

460

461

462 **Data accessibility:**

463 The data supporting the analyses are deposited online on Figshare at

464 [10.6084/m9.figshare.4557136](https://doi.org/10.6084/m9.figshare.4557136)

465

466

467 **Competing interests:**

468 We declare we have no competing interests.

469

470 **Author contributions:**

471 EV and MC conceived of the study, designed the study, and coordinated the study. EV, JS,

472 HM carried out the statistical analyses, HN carried out the molecular lab work, JS compiled

473 the pedigree, EV, MB, JG, SH, JS and HM collected field data. EV and MC drafted the

474 manuscript and all authors gave final approval for publication.

475

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654  
655 FIGURE CAPTIONS

656  
657  
658 Fig 1. Escorts care for the pups carrying, feeding, and grooming them.

659  
660 Fig. 2. Effects of group size and parentage on patterns of escorting in banded mongooses. A) Across  
661 litters, females were more likely to escort when the litter contained some of their own young, and  
662 their probability of escorting decreased with number of females in the social group (mothers = dark  
663 gray shaded area and solid line; non-mothers = light gray area and dotted line). B) Males were less  
664 likely to escort when there were more males in the social group, but whether they sired pups did not  
665 predict whether they escorted in a given litter. Lines represent model predictions  $\pm$  SE from binomial  
666 GLMMs after controlling for random effects of individual, litter and social group.

667  
668  
669 Fig. 3. Sex differences in patterns of care. A) Female escorts were more likely to pair with female  
670 pups (dark gray bars) and male escorts with male pups (light gray bars). Numbers are counts of  
671 observed escorting relationships. B) Female escorts allocated more care to female pups (dark gray  
672 area, solid line) as compared to male pups (light gray area, dotted line) when adult female group  
673 size was low. Lines in B and C represent GLMM model predictions  $\pm$  SE and dots present raw data,  
674 see SI Tables S1-S3 for full results. C) Heavier pups were more likely to be escorted and the effect of  
675 weight was more pronounced in female pups (dark gray area, solid line) than in male pups (gray area,  
676 dotted line). D) Overall, male pups received more care in existing escorting relationships than female  
677 pups, both from male and female escorts.

678

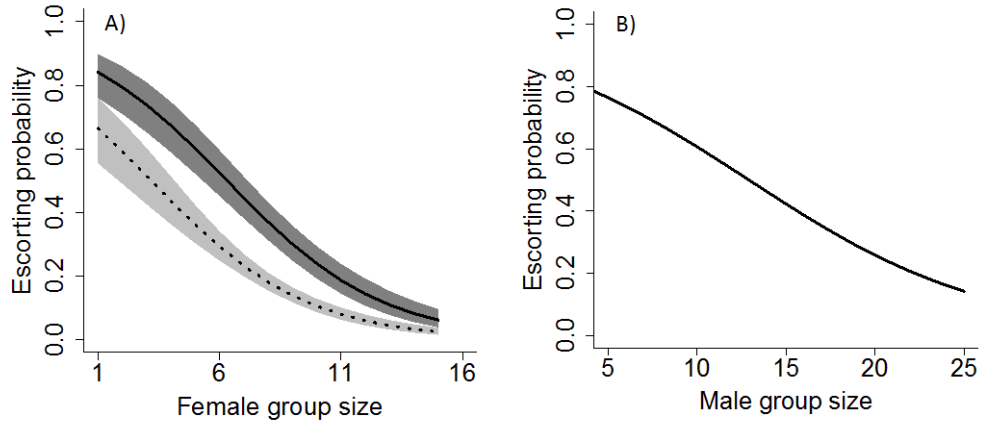
679 Figures:

680 Fig. 1



681

Fig. 2





684 Fig. 3

