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1 **Banded mongooses avoid inbreeding when mating with members**
2 **of the same natal group.**

3

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12

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18

19 Running title: Inbreeding avoidance in wild banded mongooses

20 **Abstract**

21 Inbreeding and inbreeding avoidance are key factors in the evolution of animal societies, influencing
22 dispersal and reproductive strategies which can affect relatedness structure and helping behaviours.
23 In cooperative breeding systems, individuals typically avoid inbreeding through reproductive
24 restraint and/or dispersing to breed outside their natal group. However, where groups contain
25 multiple potential mates of varying relatedness, strategies of kin recognition and mate choice may
26 be favoured. Here, we investigate male mate choice and female control of paternity in the banded
27 mongoose (*Mungos mungo*), a cooperatively-breeding mammal where both sexes are often
28 philopatric and mating between relatives is known to occur. We find evidence suggestive of
29 inbreeding depression in banded mongooses, indicative of a benefit to avoiding breeding with
30 relatives. Successfully breeding pairs were less related than expected under random mating, which
31 appeared to be driven by both male choice and female control of paternity. Male banded
32 mongooses actively guard females to gain access to mating opportunities, and this guarding
33 behaviour is preferentially directed towards less closely related females. Guard-female relatedness
34 did not affect the guard's probability of gaining reproductive success. However, where mate-guards
35 are unsuccessful they lose paternity to males that are less related to the females than themselves.
36 Together our results suggest that both sexes of banded mongoose use kin discrimination to avoid
37 inbreeding. Although this strategy appears to be rare among cooperative breeders, it may be more prominent
38 in species where relatedness to potential mates is variable, and/or where opportunities for dispersal and
39 mating outside of the group are limited.

40 Introduction

41 Breeding between relatives leads to inbreeding depression through an increase in offspring
42 homozygosity and a decrease in fitness (Charlesworth & Charlesworth 1987; Frankham 1995; Keller
43 & Waller 2002), hence inbreeding avoidance is widespread (Pusey & Wolf 1996). The likelihood of
44 encountering relatives as potential mates is particularly high in stable and/or isolated populations
45 such as those of cooperative breeders which live in extended-family groups. For cooperative
46 breeders, within-group relatedness is particularly high in groups where there is a single dominant
47 breeding pair, since in this case natal individuals are mostly first order relatives (e.g. meerkats;
48 Figure 1^{a,c}). Here, inbreeding is most commonly avoided through sex-biased philopatry: members of
49 one sex disperse in order to breed elsewhere while members of the other sex remain in their
50 natal group, preferentially breeding with immigrants or members of neighbouring groups (e.g.
51 meerkats: O’Riain et al. 2000; Young et al. 2007; pied babblers: Nelson-Flower et al. 2012; purple-
52 crowned fairy-wrens: Kingma et al. 2013; see reviews in Koenig & Haydock 2004; Lukas & Clutton-
53 brock 2011). However, in many species, groups contain multiple breeders of both sexes (Hodge
54 2009), and the degree of relatedness between natal individuals may range from very low (close to
55 zero) to very high (0.5 or higher) (e.g. banded mongooses; Figure 1^{b,d}). These circumstances might
56 favour the evolution of kin discrimination systems which allow individuals to reproduce within their
57 natal group and yet avoid breeding with siblings or other close relatives.

58 The benefits of inbreeding avoidance will typically differ for male and female breeders because of
59 sex differences in reproductive investment; in particular the energetic and opportunity costs of
60 producing poor quality offspring (Trivers 1972; Waser et al. 1986; Haig 1999). In mammals, the high
61 costs of gestation and lactation for females mean that females could gain substantial benefits from
62 inbreeding avoidance, and may be under particularly strong selection to evolve mechanisms that
63 allow them to prevent fertilisation by close male kin, for example, by rejecting mating attempts or
64 influencing the outcome of sperm competition (Hosken & Blanckenhorn 1998; Tregenza & Wedell

65 2002). Where male reproductive investment is low, male inbreeding avoidance may be expected
66 where mates are encountered simultaneously (Kokko & Ots 2006; Edward & Chapman 2011).
67 However, in species where males invest heavily in courtship, mating, or parental care they may also
68 experience substantial costs of inbreeding, and could also gain from channelling reproductive
69 investment toward unrelated females even when encountered sequentially. It is important to note,
70 however, that inbreeding is not always costly (Waser et al. 1986) or avoided (Olson et al. 2012) and
71 individuals may in fact preferentially mate with relatives if it increases inclusive fitness (Puurtilinen
72 2011; Szulkin et al. 2013). Though male mate choice has received growing attention in recent years
73 (Lihoreau et al. 2008; Edward & Chapman 2011; Lemaître et al. 2012), little is known about the
74 importance of, and possible interaction between, male and female mate choice strategies in
75 inbreeding avoidance within social groups. Investigating this question requires the study of systems
76 in which male mating effort and the level of female control over paternity can be readily observed
77 and quantified.

78 Here we investigate male mate choice and female control of paternity as potential mechanisms of
79 within-group inbreeding avoidance in a wild population of banded mongooses (*Mungos mungo*).
80 Banded mongooses are cooperative breeders that live in stable groups of 5 – 30 individuals in which
81 both sexes often breed within their natal group and many remain as breeders within their natal
82 group for their whole lives (Nichols et al. 2010; Cant et al. 2013). Within groups of banded
83 mongooses, multiple (1-10) females enter oestrous synchronously, typically in the same week
84 (Hodge, Bell, and Cant 2011). Females usually carry 3 foetuses per term (Cant 2000) but give birth
85 synchronously (usually on the same day; Hodge et al. 2009) which creates large communal litters of
86 up to 30 pups (Gilchrist 2006) which are then cared for communally by the whole group (Cant 2003).
87 During group-oestrus each female is followed closely by one or more mate-guards for periods of up
88 to several days (Nichols et al. 2010). This mate-guarding increases the chances of successful mating,
89 but females often reject the mating attempts of mate-guards and non-mate guards still gain a share
90 of paternity through sneak mating events with guarded females (Cant 2000; Nichols et al. 2010).

91 Females have been observed to mate with multiple males (up to 5) in a single breeding attempt
92 (Cant 2000), and are often guarded by different males in consecutive breeding attempts (Nichols et
93 al. 2010). The consequence of these behaviours (and philopatry of both sexes) is substantial within-
94 group variation in pairwise relatedness between males and females of breeding age (Figure 2).

95 When female banded mongooses do leave their natal group they do so in single-sex cohorts
96 following forced evictions from older, more dominant females (Cant et al. 2001). Males also leave in
97 single-sex cohorts but can do so either voluntarily or following an eviction (Cant et al. 2013). 13%
98 and 12% of males and females have been observed to leave their natal group, respectively (Cant et
99 al. 2013). New groups form when a cohort of dispersing males fuses with a cohort of females from a
100 different natal group, either by taking over a new group and evicting all current males or (if both
101 single-sex cohorts have left their natal territory) by establishing a new territory. Migration between
102 established groups is virtually absent with only 3 cases recorded in 18 groups over a period of 12
103 years (Cant et al. 2013). Though mating is skewed towards older individuals, both male and female
104 banded mongooses are capable of breeding at one year of age (Cant 2000; Nichols et al. 2010) and
105 do so often in the presence of their own parents. Females regularly conceive to close-relatives
106 including fathers and brothers (27% conceiving to a male related by 0.25 or more; Nichols et al.
107 2014). However, whether they do this less often than expected under random mating (as would be
108 the case if males and/or females exercise inbreeding avoidance) remains unclear. In the current
109 study we use a combination of behavioural and genetic data to investigate patterns of male mate
110 choice and female control of paternity to determine if banded mongooses exercise any inbreeding
111 avoidance strategies. Specifically, we address 4 questions: (1) Is there evidence of costs associated
112 with inbreeding in banded mongooses? (2) Is there evidence of inbreeding avoidance in banded
113 mongooses? (3) Is there evidence that males avoid inbreeding by directing mating effort towards
114 unrelated females? (4) Is there evidence that females avoid inbreeding through rejecting related
115 mating partners?

116

117 **Materials and Methods**

118 **Study site and data collection**

119 Behavioural and genetic data were collected from wild mongooses inhabiting the Mweya Peninsula,
120 Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E) between May 1997 and September 2013.
121 Details of vegetation and climate are available elsewhere (Cant et al. 2013). All individuals in the
122 population were habituated to the presence of human observers at 2 – 4 m, allowing the collection
123 of detailed behavioural data without any measureable effect of observer presence. Groups were
124 visited every 2 – 4 days to collect behavioural and life history data. Accurate ages (\pm 2 days) were
125 known for the majority (90%) of the population. Where accurate ages were not known (e.g. for
126 immigrants or new groups), individuals were simply classified as pups, juveniles or adults according
127 to their size, body mass and/or tooth wear (note that the majority of analyses were limited to adults)
128 (Cant, 2000). This research was carried out under licence from the Uganda National Council for
129 Science and Technology and all procedures were approved by the Uganda Wildlife Authority.

130 One or two individuals within each group were fitted with a radio collar weighing 27 g (Sirtrack Ltd.,
131 New Zealand) with a 20 cm whip antenna (Biotrack Ltd., UK). All individuals within the population
132 were marked, either with a unique shave pattern on their back or with a colour coded plastic collar.
133 Young individuals (aged less than 6 months) were marked using commercially available blonde hair
134 dye (L'Oreal, UK) to create a unique pattern on their backs. Pups were trapped within two weeks of
135 emerging from the den (aged 30 – 50 days) and all individuals within the population were trapped
136 every 3 – 6 months to maintain collars and shave/hair-dye patterns. Individuals were trapped using
137 box traps (67 x 23 x 23 cm; Tomahawk Live Trap Co., Tomahawk, WI, USA) and anaesthetised using
138 isoflurane applied through a silicon face mask or (for individuals < 6 months old) using intramuscular
139 injections of 1mg/kg of ketamine and 0.8mg/kg of medetomidine, followed by an injection of

140 0.8mg/kg of atapamezol after handling (further details of trapping protocol are given elsewhere;
141 ketamine: Hodge 2007; isoflurane: Jordan et al. 2010).

142 On first capture, permanent identification was made possible using either a uniquely coded tattoo or
143 a pit tag (TAG-P-122IJ, Wyre Micro Design Ltd., UK). A 2 mm skin sample for genetic analysis was
144 collected from the end of the tail using sterile surgical scissors. This process caused little or no
145 bleeding. After sample collection, the end of the tail was treated with a dilute solution of potassium
146 permanganate to reduce the chances of infection. This trapping protocol was used over 8000 times
147 during the course of study and genetic samples collected from 1786 individuals without any adverse
148 effects.

149

150 *Observations of mating behaviour*

151 Groups were visited daily during 211 group oestrus periods between April 2003 and September 2013
152 for observations of mating behaviour. The 'group oestrous' period (i.e. the time from the first to the
153 last day on which mating and mate-guarding was observed in a particular breeding attempt) lasted
154 3.1 ± 0.1 days (mean \pm S.E., from 211 oestrous periods). During group oestrus each female is closely
155 followed and guarded by a single male '*mate-guard*' for periods that last from several hours to several
156 consecutive days. Mate guards defend their associated female from attempts to mate by other males by
157 snapping, lunging, and pouncing towards approaching males (Nichols *et al.* 2010). These mate guarding
158 behaviours are conspicuous and are easy to identify (Cant 2000). During each observation session (1 – 5 hours;
159 1 – 2 sessions per day) all males in the group were classified as mate-guards or non-mating males (Cant
160 2000; Nichols et al. 2010) based on whether or not they engaged in mate guarding behaviors during
161 the observation session. For mate guarding males, the identity of their guarded female was also
162 recorded.

163

164 **Genetic analysis**

165 DNA was extracted from tail-tips by lysis with ProteinaseK, followed by phenol-chloroform
166 purification (Sambrook, Fritsch & Maniatis, 1989) or using DNA extraction kits (Qiagen® Tissue and
167 Blood Kit). Samples were genotyped at up to 43 microsatellite loci, isolated from a variety of
168 carnivore species, including the banded mongoose. Genotyping was conducted following (Nichols, et
169 al., 2010) or (post-2010) using multiplex PCRs (Qiagen® Multiplex PCR Kit, UK) with fluorescent-
170 labelled forward primers and were visualised through fragment size analysis on an ABI 3730 DNA
171 Analyzer. PCR conditions followed the Qiagen® Multiplex PCR Kit recommendations (but were
172 conducted in 12µl reactions), with an annealing temperature of 57°C. Full details of the 43
173 microsatellites used in this study alongside primer sequences, multiplex sets, and PCR conditions are
174 given in the supporting information (SI1.1)

175 Deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were tested
176 using Genepop 4.3 (Raymond & Rousset, 1995; Rousset2008). When tests were carried out on the full
177 dataset 33/43 loci and 826/903 pairs of loci were found to deviate from HWE and LD, respectively (see SI1.1;
178 table SI1.1.4). However, when tests were carried out on 300 randomised subpopulations of non-relatives, no
179 loci or pairs of loci were found to consistently deviate from HWE or LD (see SI1.1; tables SI1.1.4 & SI1.1.5). All
180 loci were manually checked for sex-linkage by comparing a subset of male and female genotypes. Full details
181 of allele frequencies as well as expected and observed heterozygosity values are given in the
182 supporting information (SI2).

183 We generated a 9-generation deep pedigree using familial relationships within the banded
184 mongoose research project study population inferred using field observations, individual genotypes,
185 and two freely available programs; MasterBayes 2.51 (Hadfield et al. 2006), which was implemented
186 in R 3.1.1 (R Core Team, 2013), and COLONY 2.0.5.7 (Jones & Wang 2010). Full details of pedigree
187 construction are given in the supporting information (SI1.2).

188 In brief, we first used MasterBayes (Hadfield et al. 2006) to assign parents to 2633 individuals
189 classified as offspring (i.e. individuals that were observed being born into the population, 2633 from
190 a total of 2878 individual recorded in the population), of which 1593 were genotyped. All females
191 (aged > 6 months) present in the offspring's natal group at birth were included as candidate mothers
192 and all males (aged > 6 months) present in the study population at conception were included as
193 candidate fathers to allow for extra-group mating. We also included the following phenotypic
194 predictors of parentage: whether or not a female was recorded as giving birth, if a male was in the
195 offspring's natal group prior to birth, and the age and quadratic age of both males and females. The
196 numbers of unsampled candidate mothers and fathers were estimated in the parentage assignment
197 model. Genotyping error rates were calculated manually from samples that were genotyped in
198 duplicate following Hoffman & Amos (2005). Allele frequencies were calculated in Cervus 3.0.7
199 (Kalinowski et al. 2007) using the full genotype data set. These genotyping error rates and allele
200 frequencies were provided in the model specification. The Markov chain Monte Carlo estimation
201 chain was run for 1,500,000 iterations with a thinning interval of 500, and a burn-in of 500,000. No
202 further prior distributions were specified and default improper priors were used. Successive samples
203 from the posterior distribution had low autocorrelation ($r < 0.01$).

204 Secondly, sibships were constructed in COLONY (Jones & Wang 2010) by partitioning all 1787
205 genotyped individuals (including offspring, founders, and immigrants) into full- and half-sibship
206 groups with or without parentage assignments, using a maximum likelihood method. The same
207 candidate parent criteria were used as above to generate candidate father list, candidate mother list,
208 paternal exclusion list and maternal exclusion list as input into Colony. No maternal or paternal
209 sibships were excluded. A weak sibship prior of 1.5 for both maternal and paternal average sibship
210 size was included to limit false-positive sibship assignments, and the probabilities that the true
211 mother and father were in the candidate lists were both set as 0.8 (see figure S2.1).

212 Parentage assignment was accepted with ≥ 0.8 probability in both MasterBayes and Colony.
213 MasterBayes parentage assignments were accepted first (1474 assigned maternities and 1397
214 assigned maternities, note that no ungenotyped individuals were confidently assigned parentage)
215 and Colony parentage assignments were then added where MasterBayes had failed to assign
216 parentage (a further 29 maternities and 45 paternities). Note that of the 1200 and 1029 cases in
217 which both MasterBayes and Colony assigned maternity and paternity, only 55 and 69 were
218 mismatched, respectively. Following this, we used the full-sibships assigned using Colony to infer
219 maternity and paternity to a further 67 and 34 offspring, respectively (see supporting information
220 for further details; SI1.2). These assignment rules allowed us to infer a 9-generation deep pedigree
221 which includes 1570 maternities and 1476 paternities.

222 Using the same panel of genetic markers for parentage assignment and for calculating levels of
223 relatedness has been shown to bias paternity assignments towards unrelated fathers in some cases
224 (Wang 2010). We minimised the probability of encountering such biases by using a large panel of
225 markers for parentage analysis (43 microsatellites) which allowed for high confidence of parentage
226 assignment in almost all cases; of the 1083 offspring genotyped during the period of behavioural
227 observations (between April 2003 and September 2013), 986 and 955 (91% and 88%) were assigned
228 paternity at ≥ 0.8 and ≥ 0.95 , [PubMed](#) respectively (see supporting information 1.3 for further details
229 of testing for biases in parentage assignment). Furthermore, where possible, we verified our genetic
230 data using behavioural observations of mate-guarding patterns, which are not subject to such biases.

231

232 **Statistical analyses**

233 1. Is there evidence of costs associated with inbreeding in banded mongooses?

234 To test for possible costs associated with inbreeding in banded mongooses we modelled its effect on
235 two variables which are likely to be associated with fitness: yearling body mass and survival to 1 year.

236 Pedigree-based inbreeding coefficients (F) were available for 1001 individuals (with assigned parents)
237 born between March 2003 and September 2013. In total, 425 of the individuals included in these
238 analyses had non-zero inbreeding coefficients.

239 Overall, 777 observations of body mass were available from 210 yearlings (aged between 350 and
240 370 days) from 79 breeding attempts and 9 social groups. This yearling body mass was fitted as a
241 response in a GLMM with inbreeding coefficient as the main predictor of interest along with age in
242 days to control for differences in age at measurement. Further to this, data on survival to 1 year of
243 age was available for 839 individuals from 183 breeding attempts in 13 social groups. This survival to
244 independence was fitted as a binomial response in a GLMM, again with inbreeding coefficient as the
245 main predictor of interest. Mean daily rainfall in the 30 days prior to birth, maternal age (months),
246 the number of pups born in the same litter as the observed individual, and group size at the time of
247 birth (number of individuals aged > one year) were also fitted as fixed effects in both models to
248 control for their possible effects on both response traits. Social group, breeding attempt, maternal
249 identity and paternal identity were fitted as random factors in both models to control for repeated
250 measures as well as an individual identity in the body mass model to control for
251 repeated observations of the same individual.

252

253 2. Is there evidence of inbreeding avoidance in banded mongooses?

254 To test whether banded mongooses preferentially mate with non-relatives from within their social
255 group, we compared pairwise relatedness estimates from observed breeding pairs with pairwise
256 relatedness estimates from simulated male-female dyads under random mating. Specifically, we
257 created randomizations of male-female dyads by assigning each female (with assigned maternity) to
258 a random adult male (aged > 1 year) from within the same social group. If a female had multiple
259 pups sired by the same male within a breeding attempt then this was counted as a single male-

260 female breeding pair and the female was only assigned one random male within each permutation.
261 If a female had pups assigned to more than one male within a breeding attempt she was assigned
262 the same number of random males. Data were available from 624 successful breeding pairs of
263 banded mongooses from 196 breeding attempts in 16 different social groups. However, we limited
264 this dataset to 269 breeding pairs which satisfied the following criteria: (1) mother had both parents
265 confidently assigned (452/624 observations); (2) at least 80% of candidate fathers had confidently
266 assigned parents (395/624 observations); (3) the male with assigned paternity was from the same
267 group as the female assigned maternity (i.e. within-group mating; 400/624 observations). Exclusion
268 criteria 1 and 2 reduced noise associated with including pedigree-derived relatedness coefficients
269 from individuals with unknown parentage in randomisations while exclusion criteria 3 allowed us to
270 test for inbreeding avoidance in the absence of any effects of extra-group mating. Within each
271 permutation we calculated the mean pairwise relatedness of 269 randomized male-female dyads.
272 Raw values from the 269 observed male-female dyads were compared to null distributions
273 generated from 10,000 permutations of the data to derive a 1-tailed P-value.

274 As we are interested in inbreeding avoidance in the absence of any cues of familiarity (i.e. within-
275 versus extra-group individuals and/or natal- versus non-natal individuals) we repeated these
276 simulations limiting the data set to 137 breeding attempts where both all adult males and all adult
277 females were observed to have been born within the same social group. This further conservative
278 analysis allowed us to clarify if inbreeding avoidance occurs in the absence of cues of familiarity
279 which may be present in newly formed groups or those which have recently accepted immigrants.
280 Here, estimates of relatedness were available from 439 observed male-female dyads which was then
281 limited to 201 following the same criteria as above (criteria 1: 328/439; criteria 2: 306/439; criteria 3:
282 276/439); raw values from these 201 observed male-female dyads were compared to null
283 distributions generated from 10,000 permutations of this dataset of natal individuals to derive a 1-
284 tailed P-value.

285

286 3. Is there evidence that males avoid inbreeding by directing mating effort towards unrelated
287 females?

288 To test whether male banded mongooses preferentially direct guarding effort towards unrelated
289 females we compared pairwise relatedness estimates from observed guard-female dyads with
290 pairwise relatedness estimates from simulated guard-female dyads under random mating.
291 Specifically, we created randomizations of guard-female dyads by assigning males that had been
292 observed mate-guarding to a random guarded female from within the same oestrus event. If a male
293 was observed to guard more than one female within an oestrus event he was randomly assigned the
294 same number of females, similarly if a female was guarded by more than one male then the same
295 number of guards were assigned to her. Data were available from 1074 observed guard-female pairs
296 from 212 oestrus events in 13 different social groups. However, (similar to the analyses above) we
297 limited this dataset to 649 guard-female pairs which satisfied the following criteria: (1) the mate-
298 guard had confidently assigned parents (866/1074 observations); (2) at least 80% of candidate
299 females had confidently assigned parents (738/1074 observations). Within each permutation we
300 calculated the mean pairwise relatedness of 684 randomized guard-female dyads. Raw values were
301 compared to null distributions generated from 10,000 permutations of the data to derive a 1-tailed
302 *P*-value.

303 Again, as we are interested in whether or not male banded mongooses are able to direct their
304 mating effort towards unrelated females in the absence of simple cues of familiarity (i.e. group
305 membership) we repeated these simulations limiting the data set to 175 breeding attempts where
306 all adult females were observed to be born within the same natal group. Here, estimates of
307 relatedness were available from 842 observed guard-female dyads which was then limited to 481
308 following the same criteria as above (criteria 1: 686/842; criteria 2: 548/842); raw values from these

309 481 observed guard-female dyads were compared to null distributions generated from 10,000
310 permutations of this dataset of natal individuals to derive a 1-tailed P-value.

311

312 4. Is there evidence that females avoid inbreeding through rejecting related mating partners?

313 Previous behavioural observations indicate that females sometimes reject the copulation attempts
314 of their mate guards (Cant 2000), and so may plausibly influence control over the distribution of
315 paternity among males by rejecting mating attempts. Females could also exercise cryptic mate
316 choice by influencing the probability of fertilisation or successful implantation post-copulation. To
317 evaluate the degree to which females can influence the distribution of paternity we investigated (1)
318 whether males observed guarding unrelated females were more likely to be successful in gaining
319 paternity than males guarding related females and (2) where mate guards were not successful in
320 gaining paternity we compared the relatedness of the mate-guard and extra-pair paternity male
321 (EPP) to the female to test whether females were 'upgrading' to males they were less related to.

322 In total, 234 mate-guard identities were observed for 171 females which were confidently assigned
323 at least one offspring within 40 – 80 days of observed oestrus (note that females were often guarded
324 by more than one male per oestrus period). Within each of these mate-guard-female pairs the mate-
325 guard was categorised as 'successful' or 'unsuccessful' at reproducing with that female if it did or did
326 not gain paternity, respectively. We further limited this data set to 159 pairs of mate-guard and
327 female identities which both had confidently assigned parents and were of known age/age rank (mate
328 guard with assigned parents: 193/234; female with assigned parents: 187/234; guard known age rank:
329 212/234; female known age: 220/234). These exclusion criteria reduced noise associated with using
330 pedigree-derived relatedness from individual without assigned parents and allowed us to test for
331 variation in mate-guard success while controlling for any effects of age (Nichols et al. 2010). If
332 females do exert control over paternity as a strategy to avoid inbreeding then we expect males to be

333 more successful when guarding an unrelated female. Paternity success was fitted as a binomial
334 response in a GLMM with guard-female relatedness as the main predictor of interest. Male age rank,
335 female age, sex ratio, and the number of days spent guarding were also fitted as fixed effects to
336 control for any effects on mate-guard success. In order to exclude any possibility that females may
337 use natal group membership as cues to relatedness when exerting control over paternity of their
338 offspring we repeated this analysis with 116 mate-guard-female pairs in which all within group males
339 were observed to be born within the same natal group and the above criteria were again followed.

340 From the 234 observed guard-female pairs, 160 were of mate-guard identities which did not match
341 any offspring assigned to that female within that breeding attempt (i.e. indicative of extra-pair
342 paternity; EPP). This dataset was limited to 114 mate-guard-female pairs where the identities of
343 parents were confidently assigned for the mate-guard, female, and the EPP male (mate-guard with
344 assigned parents: 138/160; female with assigned parents: 131/160, EPP male with assigned parents:
345 138/160). Furthermore, we excluded another 12 cases where there were 2 assigned EPP identities
346 which did not match the mate guard identity to allow for a direct pairwise comparison per breeding
347 event (leaving a total of 102 paired relatedness values for analysis). We compared the relatedness of
348 mate-guard-female pairs with that of EPP male-female pairs using paired t-tests. Females may avoid
349 inbreeding either by mating with unrelated males within their own group or by mating with extra-
350 group males (Nichols et al, in prep). To examine if females exert control over paternity towards
351 unrelated males while still mating within their own group we categorised the EPP males as within-
352 group (WG) or extra-group (EG) and carried out 2 further t-tests limited to either within-group or
353 extra-group EPP males. We also repeated these analyses with data limited to 89 guard-female pairs
354 in social groups where all males were known to be from the same natal group and the above criteria
355 were satisfied.

356 All statistical analyses were carried out using R 3.0.1 (R Core Team, 2013). We used generalised
357 linear mixed models (GLMMs) to control for repeated measures within social groups, breeding

358 attempts, and individuals fitted using the lme4 package (Bates, Maechler, & Bolker, 2013).
359 Binomially distributed response variables were analysed with a logit link function. Explanatory
360 variables were sequentially dropped from the model until only those variables explaining significant
361 variation ($p < 0.05$) remained following Crawley (2012). All dropped variables were then individually
362 put back into the minimal model to determine their level of non-significance. Social group, breeding
363 attempt, and male and female identities were included as random effects in all analyses where
364 appropriate.

365

366 **Results**

367 1. Is there evidence of costs associated with inbreeding in banded mongooses?

368 Yearling body mass decreased with increase in the inbreeding coefficient (GLMM; $\chi^2_{(1)} = 5.29$, $p =$
369 0.021 ; figure 3) suggestive of a cost to inbreeding. Variation in age at capture had an effect on
370 weight (GLMM; $\chi^2_{(1)} = 11.64$, $p = 0.0006$) but there was no effect of the number of pups, rainfall,
371 group size, or maternal age on pup body mass at 1 year of age (table 1).

372 We found no effect of inbreeding on the likelihood of survival to 1 year of age (GLMM; $\chi^2_{(1)} < 0.001$,
373 $p = 0.99$), nor was there any effect of group size, maternal age or the number of pups (table 1).
374 Banded mongooses were more likely to survive to one year of age when daily rainfall 30 days prior
375 to their birth was high (GLMM; $\chi^2_{(1)} = 8.09$, $p = 0.004$).

376

377 2. Is there evidence of inbreeding avoidance in banded mongooses?

378 If male and/or female banded mongooses use kin discrimination to avoid mating with relatives and
379 the associated inbreeding costs, we expect females to mate with males that are less related to them
380 than expected under random pairing. The observed mean relatedness between breeding male-

381 female pairs was lower than expected by chance both when all data was considered (observed value
382 = 0.15, null distribution mean = 0.18, $P = 0.002$; Figure 4^a) and when data was limited to breeding
383 attempts where all adult males and all adult females were from the same natal group (observed
384 value = 0.17, null distribution mean = 0.19, $P = 0.019$; Figure 4^b).

385

386 3. Is there evidence that males avoid inbreeding by directing mating effort towards unrelated
387 females?

388 If males direct mating effort towards unrelated females, we predict males to guard females that are
389 less related to them than expected under random pairing. The observed mean relatedness between
390 mate-guards and guarded females was lower than expected by chance when analysing the complete
391 dataset (observed value = 0.16, null distribution mean = 0.17, $P = 0.007$; Figure 5^a). However, when
392 analysis was limited to breeding attempts where all females were from the same natal group (i.e.
393 mate guards had no access to simple cues of familiarity) we only found a trend for males to mate-
394 guard females who are less related to them than expected by chance (observed value = 0.18, null
395 distribution mean = 0.19, $P = 0.072$; Figure 5^b).

396

397 4. Is there evidence that females avoid inbreeding through rejecting related mating partners?

398 Mate guards were no more likely to be successful at gaining paternity when guarding a female of
399 lower relatedness (GLMM; $\chi^2_{(1)} = 3.01$, $P = 0.083$), implying that females do not exert control over
400 paternity of their offspring with respect to relatedness (either through pre- or post-copulatory mate
401 choice). Older ranked guards were more likely to be successful at gaining paternity than younger age
402 ranked guards (GLMM; $\chi^2_{(1)} = 6.35$, $P = 0.012$), and increased number of days spent guarding
403 increased a guards chance of success ($\chi^2_{(1)} = 6.51$, $p = 0.011$). Neither female age nor the group sex
404 ratio had an effect on a mate guard's likelihood of gaining reproductive success with the guarded

405 female (table 2). When analyses were restricted to females that had no access to simple rules of
406 familiarity (all within group males were of the same natal group) we obtained qualitatively similar
407 results (table 2).

408 When paternity was assigned to a male which did not match the observed mate-guarding male (i.e.
409 extra-pair paternity; EPP), females were less related to the EPP male than they were to their mate
410 guard (t-test: $t_{101} = 4.19$, $P < 0.001$; figure 6). Furthermore, this difference remained significant when
411 considering only within- or extra-group EPPs (t-test; within-group extra-pair paternity: $t_{80} = 2.47$, $P =$
412 0.016 ; extra-group extra-pair paternity: $t_{20} = 4.54$, $P < 0.001$; figure 6). Again, qualitatively very
413 similar results were obtained when these analyses were restricted to females that had no simple
414 familiarity cues to relatedness (t-tests: mate-guard vs. extra-pair paternity: $t_{88} = 4.03$, $P < 0.001$;
415 mate-guard vs. within-group extra-pair paternity: $t_{71} = 2.60$, $P = 0.011$; mate-guard vs. extra-group
416 extra-pair paternity: $t_{16} = 3.85$, $P = 0.001$).

417

418 **Discussion**

419 Our findings demonstrate patterns of inbreeding avoidance in a wild population of banded
420 mongooses. To our knowledge, we are the first to describe a cooperative breeding system where
421 inbreeding avoidance can occur even in the absence of dispersal or mating between groups. We
422 found that inbred pups were lighter at one year of age. Given that early-life body mass is a strong
423 predictor of adult fecundity (Hodge 2005), this is highly indicative of a cost to inbreeding in banded
424 mongooses. Successfully breeding pairs, identified through genetic parentage analysis, were found
425 to be less related than expected under random mating. Male banded mongooses directed mating
426 effort (mate-guarding) towards unrelated females indicating that males are able to discriminate
427 between relatives and use selective mate choice to avoid inbreeding. Furthermore, males guarding
428 unrelated females were no more likely to be successful than males guarding related females.

429 However, when mate-guards were unsuccessful we found that paternity was assigned to males that
430 were less related to the female than her mate-guard. These results suggest that though males
431 preferentially direct their mating effort towards unrelated females, females themselves also actively
432 avoid inbreeding through exerting control over paternity. Together our results are strongly
433 suggestive of an ability to discriminate between relatives and avoid inbreeding for both male and
434 female banded mongooses even when mating with individuals from the same natal group.

435 One potential difficulty for studies of inbreeding is that it may be more difficult to assign paternity of
436 offspring to males that are more closely related to their female mates, leading to inflated estimates
437 of the relative reproductive success of unrelated compared to related males (Wang 2010). This may
438 be particularly likely when the true father has not been sampled, resulting in an assignment being
439 made at low confidence to the incorrect male. In the current study, 93% of candidate fathers were
440 genotyped and 91% of offspring were confidently assigned paternity. Though we found a significant
441 negative effect of parent relatedness on the confidence of MasterBayes paternity assignment, the
442 effect size was very small with parents that were first order relatives (i.e. $r = 0.5$) expected to have a
443 paternity assignment with confidence reduced by 0.04 compared to paternity assignment between
444 non-relatives (i.e. $r = 0$) (see SI1.3 for further details). We interpret this as suggestive that any bias in
445 paternity assignment towards unrelated males is unlikely to affect our downstream analyses given
446 the high proportion of offspring assigned confident parentage in our pedigree. A second difficulty for
447 inbreeding studies is that intense inbreeding depression, such as selective abortion and/or increased
448 mortality of inbred pups, could generate results compatible with reproductive skew towards
449 unrelated males if the highly inbred offspring of related males rarely survive. As female banded
450 mongooses give birth synchronously in inaccessible underground dens, sampling or even counting
451 offspring within the communal litter is impossible until they emerge at ~ 30 days of age (Cant et al.
452 2013). Therefore, we cannot reject the possibility that the results presented for questions 2 and 4
453 could also arise from differential survival between inbred and outbred pups. Unrelated mating pairs
454 experiencing higher reproductive success could therefore reflect inbreeding avoidance, inbreeding

455 depression or combination of the two. However, as the methods used to address question 3 only use
456 behavioural data there is still evidence for within-group inbreeding avoidance even if differential
457 survival accounts for the results presented for questions 2 and 4.

458 An individual's ability to choose an unrelated mating partner is reliant on accurate mechanisms of
459 kin discrimination. This may be through rules of familiarity (Clarke & Faulkes 1999; Frommen et al.
460 2007) or self-referential cues (Mateo 2010; Thünken et al. 2013). Where there are high levels of
461 promiscuity and reproductive synchrony, such as in the banded mongoose (Cant 2000; Hodge et al.
462 2011), familiarity may be an unreliable indicator of relatedness and so individuals are more likely to
463 use self-referent cues to find an unrelated mating partner. Examples include major urinary proteins
464 (MUPs, Hurst et al., 2001; Sherborne et al., 2007) and other odours linked to the major
465 histocompatibility complex (MHC; Gerlach & Lysiak, 2006; Havlicek & Roberts, 2009; Leclaire et al.,
466 2014). Banded mongooses use scent from anal gland secretions to communicate both within and
467 between groups (Müller & Manser 2007; Jordan et al. 2010, 2011) and show marked between
468 individual variation in scent profiles (Jordan et al. 2011), suggesting that they may use scent as a cue
469 to relatedness (as seen in meerkats; Leclaire et al. 2013). Furthermore, banded mongooses emit
470 highly frequent vocal contact calls which contain individually identifiable signatures (Jansen et al.
471 2013) and it is also possible that vocal signatures act as a cue to relatedness (Penn & Frommen 2010).

472 The costs of inbreeding are expected to be highest for individuals with high reproductive investment.
473 For many species, the energetic costs associated with gamete production and offspring care mean
474 that reproductive investment is highest in females (Trivers 1972; Haig 1999). However, males can
475 also sometimes invest heavily in reproduction, both through mating effort and investment in
476 offspring care. Male banded mongooses guard females for multiple consecutive days in order to gain
477 access to paternity. This guarding behaviour involves costly aggressive interactions (Cant 2000;
478 Nichols et al. 2010) and reduces the time available for foraging (Sanderson, pers. obs.). Furthermore,
479 male banded mongooses also invest heavily in offspring care; often even more so than females

480 (Hodge 2007). This high reproductive investment suggests that male banded mongooses may also
481 experience high fitness costs associated with inbreeding, which could explain why males are
482 observed to preferentially guard unrelated females. Male mate choice is also predicted to occur
483 where there is variation in female quality and where receptive females are encountered
484 simultaneously (Edward & Chapman 2011). Indeed, high levels of promiscuity within banded
485 mongoose societies means that males have access to females which vary in genetic compatibility
486 and the high degree of female reproductive synchrony seen within banded mongoose groups (Hodge
487 et al. 2011) means that males do encounter receptive females simultaneously. The extent to which
488 females synchronise breeding within-groups could in fact promote male choice even in the absence
489 of high male reproductive investment as male mating opportunities are limited by the fact that they
490 can only guard one female at a time. Together, these factors are indicative of a breeding system
491 where male choosiness is predicted and highlight the possibility that the non-random pairing seen in
492 this study may be a result of male mate choice to avoid fitness costs associated with inbreeding.

493 The probability of reproductive success for guarding males (measured as whether or not a mate-
494 guard was assigned paternity) was found to be independent of relatedness to the guarded females,
495 suggesting that females are no more likely to reject the mating attempts of related guards. However,
496 where mate-guards were unsuccessful they lost paternity to males that were less related to the
497 females than themselves. Though this pattern may be driven by differential offspring survival (see
498 above) it indicates that females may direct paternity away from their mate-guards when there is an
499 opportunity to upgrade to a less related male. Where females are able to influence paternity of their
500 offspring (e.g. through post-copulatory mechanisms such as sperm competition; Simmons 2005
501 and/or selective abortion; Thomas et al. 1985), this may also influence the optimal mate choice
502 strategies of males (Tennenhouse 2014); males have little to gain through investment in mate
503 guarding or fighting to monopolise access to a particular female if she then rejects him as a mate or
504 reduces his fertilisation success post-copulation. This means that males may be observed to
505 preferentially direct mating effort towards unrelated females even in the absence of any inbreeding

506 costs to themselves. However, given the high reproductive investment of male banded mongooses
507 (both mate-guarding and offspring care; Gilchrist & Russell, 2007; Hodge, 2007; Nichols, Amos, Cant,
508 Bell, & Hodge, 2010) it seems more likely that male mate choice has evolved as a male inbreeding
509 avoidance strategy rather than a response to female choice.

510 Individuals living within stable social groups frequently encounter close relatives as potential mates.
511 How individuals respond to this can have profound effects on population processes. Previous studies
512 of inbreeding avoidance in cooperatively breeding species have focused on reproductive suppression
513 and sex-biased philopatry (Blouin & Blouin 1988; Lukas & Clutton-brock 2011; Nelson-Flower et al.
514 2012). Though banded mongooses do sometimes breed with close relatives, and often breed with
515 more distant relatives (Nichols et al. 2014), we have shown here that individuals may also avoid
516 inbreeding through selective mate choice. Banded mongooses do not exhibit sex-biased philopatry;
517 both sexes commonly breed within their natal group and remain there for their whole lives (Cant et
518 al. 2013). Thus, the ability to discriminate between kin and non-kin within individuals of the same
519 natal group may allow banded mongooses to avoid the potentially high costs of dispersal while still
520 avoiding any fitness consequences of inbreeding. This mechanism of inbreeding avoidance is
521 previously unknown in cooperative breeders (Lukas & Clutton-brock 2011), but may be more
522 important in species where there is variation in within-group relatedness, and where dispersal or
523 extra-group mating opportunities are limited.

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528

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535 **Author Contributions**

536 JLS & HN designed the research; H.N. carried out the genetic analyses; JLS analysed the data with
537 assistance from HN; JW carried out the sibship and parentage assignments in Colony; JLS, MAC, &
538 HN wrote the paper with comments from EV and JW; field data collection was carried out by EV,
539 MAC, and JLS.

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683

684 **Data accessibility**

685 DNA sequences for the microsatellite loci: Genbank accessions AF271115, AF271117, AF271118,
686 AF271120, AY142693, AY142694, AY142696, AY142697, AY142700, AY142703, AY155580, AY090498,
687 EU045417, EU045419, KP895833, KP895834, KP895835, KP895836, KP895837, KP895838, KP895839,
688 KP895840, KP895841, KP895842, KP895843, KP895844, KP895845, KP895846, KP895848, KP895849,
689 KP895850, KP895851, KP895852. JF746985, ERP000497, JF746989. See Table SI1.1.1 for further
690 details.

691 Microsatellite genotypes, pedigree, relatedness estimates, inbreeding coefficients, and behavioural
692 data: Dryad doi:10.5061/dryad.gc371

693 **Table 1.** Effects of inbreeding on body mass and survival to 1 year of age. Significant results are given in bold. Social group, litter, paternal and maternal
 694 identities were included as random effects in both models as random effects as well as individual identity in the model testing yearling body mass.

Explanatory terms	Yearling Body Mass (aged 350 - 370 days)				Survival to 1 Year of Age			
	Effect Size ± SE		χ^2	p	Effect Size ± SE		χ^2	p
Inbreeding coefficient	-347.9	± 143.4	5.29	0.02	-0.03	± 0.23	< 0.001	0.99
Maternal age	0.70	± 0.42	2.84	0.09	0.00	± 0.00	0.46	0.50
Group size	2.23	± 2.08	1.11	0.29	-0.01	± 0.02	0.52	0.47
Number of pups	1.13	± 2.30	0.22	0.64	0.02	± 0.01	1.51	0.22
Rainfall	-4.51	± 6.62	0.64	0.42	0.20	± 0.07	8.09	0.004
Age (days)	1.15	± 0.22	11.64	< 0.001			NA	
Constant	807.5	± 127.9			-1.31	± 0.22		

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698 **Table 2.** Factors affecting mate-guard likelihood of gaining paternity with guarded female for (i) all females and (ii) only females with no access to simple
699 rules of familiarity (i.e. relatedness dependent on natal group membership). Effect sizes are given on the logit scale. Significant results are given in bold. .
700 Social group, breeding attempt, guard and female identities were included as random effects in both models as random effects.

Explanatory terms	All females				Females with no access to familiarity cues of relatedness			
	Effect Size ± SE		χ^2	p	Effect Size ± SE		χ^2	p
Guard-female relatedness	-2.60	± 1.63	3.01	0.083	0.73	± 1.48	0.24	0.63
Male age rank	-0.20	± 0.09	6.35	0.012	-0.14	± 0.09	2.88	0.089
Female age	0.02	± 0.01	1.81	0.18	0.02	± 0.01	3.63	0.057
Group sex ratio (% male)	3.89	± 3.19	1.67	0.20	4.31	± 4.41	1.07	0.30
Number of guarding days	0.52	± 0.22	6.51	0.011	0.81	± 0.29	9.86	0.0017
Constant	-1.05	± 0.58			-2.76	± 0.62		

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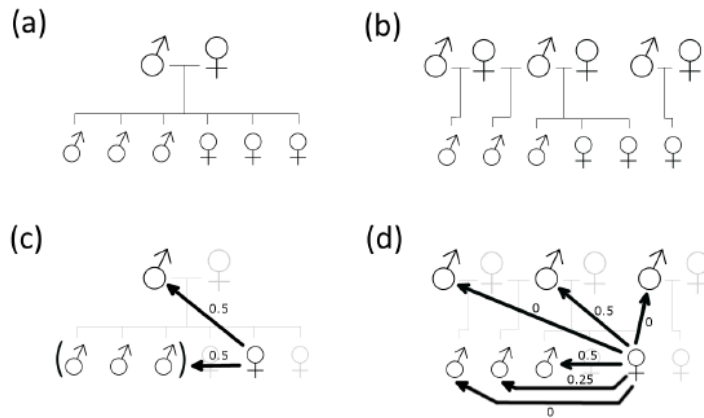


Figure 1. Differences in within-group relatedness structure between meerkats (*Suricata suricatta*) and banded mongooses (*Mungos mungo*) may be attributable to differences in reproductive skew. Schematics of single breeding attempts within (a) meerkat and (b) banded mongoose social groups are shown with lines representing pedigree. Relatedness values of a single philopatric female to within-group males after this single breeding attempt are shown for social groups of (c) meerkats and (d) banded mongooses. Meerkats have high reproductive skew with a stable breeding pair while banded mongooses breed promiscuously with low reproductive skew; philopatric meerkat females do not have access to unrelated mating partners within their social group (except for immigrant males) whereas philopatric banded mongoose females do.

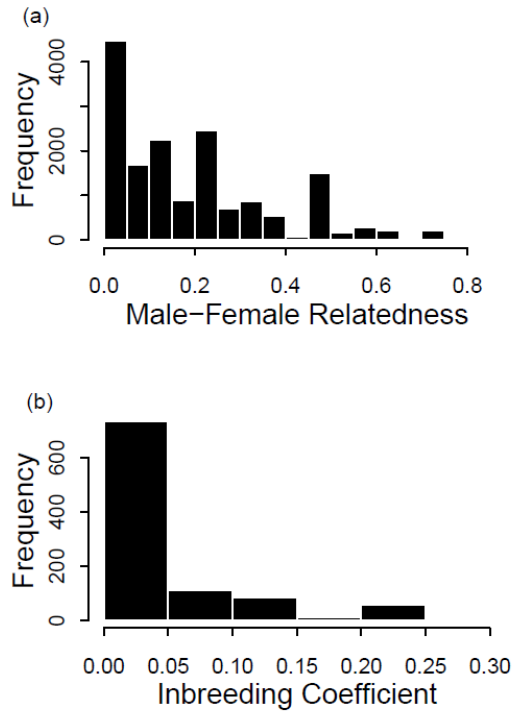


Figure 2. Histograms of (a) pairwise relatedness values from within-group male-female pairs and (b) offspring inbreeding coefficients. (a) Estimates of pedigree-based relatedness from adult (aged > 1 year) males and females present within 419 observed breeding attempts (total number of possible pairs = 16,327; including 268 unique male identities and 185 unique female identities). (b) Pedigree-based inbreeding coefficients from 1001 offspring with assigned parents. Note that 1 individual had an inbreeding coefficient of 0.375 but is excluded from the figure because it was not visible at this scale.

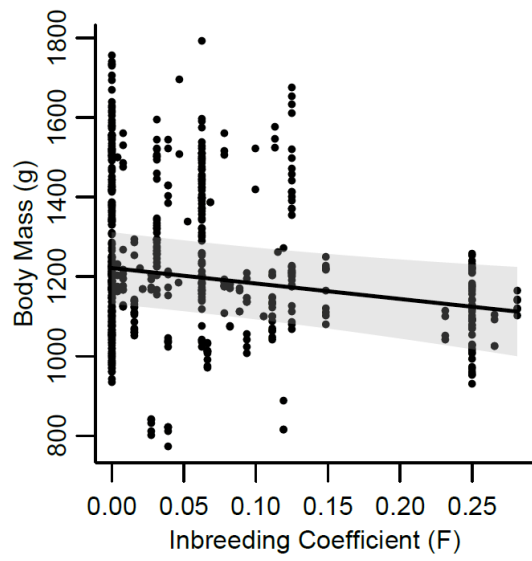


Figure 3. Relationship between inbreeding and body mass (g) in banded mongooses aged between 350 and 370 days. Dots show raw values. Line and shaded area show predicted mean and standard error estimated from a GLMM controlling for a significant effect of age.

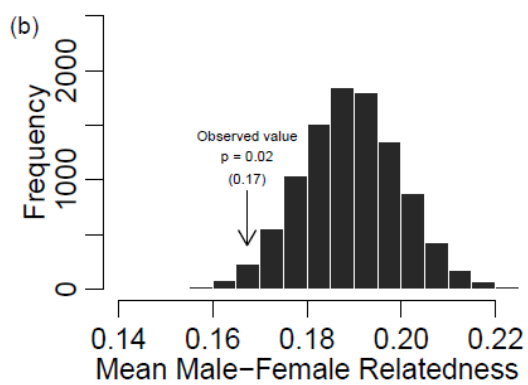
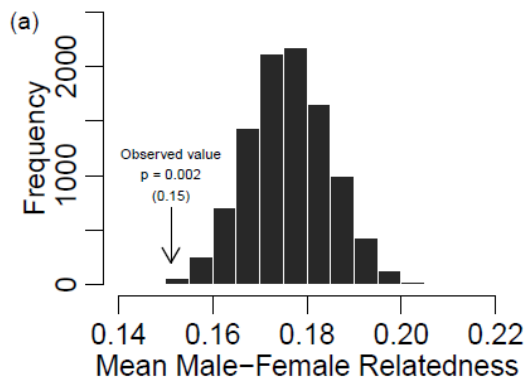


Figure 4. Randomisation histograms of the null distribution of mean male-female pairwise relatedness if females were to randomly mate with adult males within their group; (a) when all breeding attempts are considered and (b) when only breeding attempts with single-sex cohorts from the same natal group were considered.

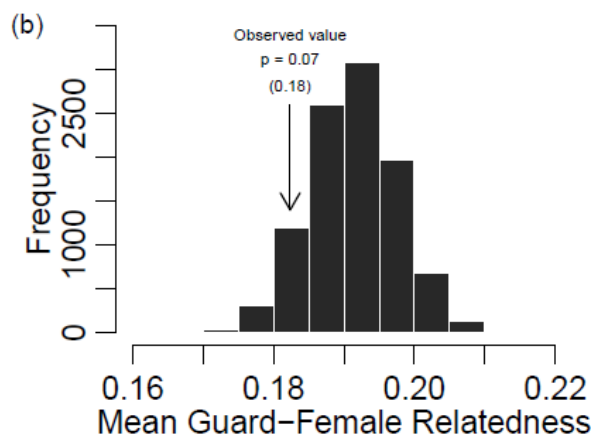
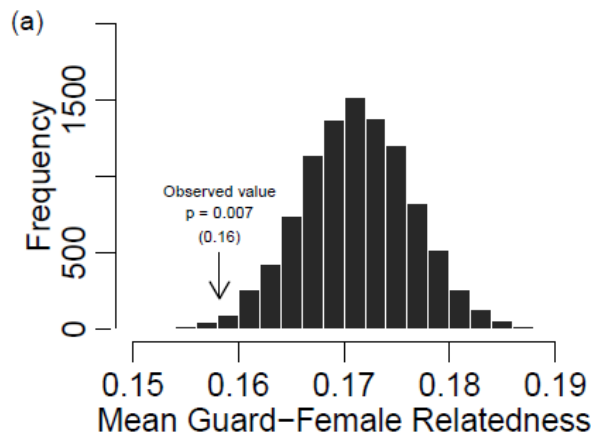


Figure 5. Randomisation histograms of the null distributions of mean guard-female pairwise relatedness if males were to randomly guard receptive females within their group; (a) when all breeding attempts were considered and (b) when analyses were restricted to breeding attempts where all females were from that same natal group.

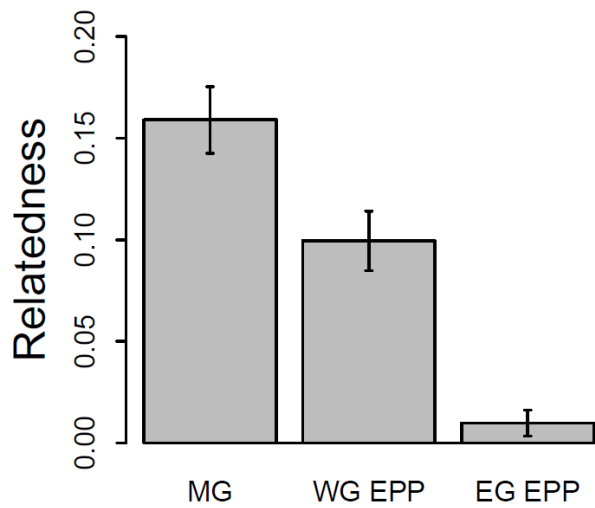


Figure 6. Relatedness estimates of a female to the observed mate guard (MG; $n = 102$), within-group extra-pair paternity (WG EPP; $n = 81$), and extra-group extra-pair paternity (EG EPP; $n = 21$) where the paternal identity did not match the observed mate guard identity. Bars show mean values and error bars show standard errors. Female relatedness to the EPP male was significantly lower than that to the observed mate-guard both with mating within- and extra-group.