



Swansea University  
Prifysgol Abertawe



## Cronfa - Swansea University Open Access Repository

---

This is an author produced version of a paper published in:  
*Behavioral Ecology*

Cronfa URL for this paper:  
<http://cronfa.swan.ac.uk/Record/cronfa44734>

---

### **Paper:**

Nichols, H., Cant, M. & Sanderson, J. (2015). Adjustment of costly extra-group paternity according to inbreeding risk in a cooperative mammal. *Behavioral Ecology*, 26(6), 1486-1494.  
<http://dx.doi.org/10.1093/beheco/arv095>

---

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

# **Adjustment of costly extra-group paternity according to inbreeding risk in a cooperative mammal**

**Hazel J Nichols<sup>1\*</sup>, Michael A Cant<sup>2</sup>, Jennifer L Sanderson<sup>2</sup>**

1. School of Natural Science and Psychology, Liverpool John Moores University, UK.

2. College of Life and Environmental Sciences, University of Exeter, UK.

\*corresponding author

Corresponding Author: Hazel J Nichols. School of Natural Science and Psychology, Liverpool John Moores University, Liverpool, UK, L3 3AF. Tel: +44 (0)151 231 2376. Email: [h.j.nichols@ljmu.ac.uk](mailto:h.j.nichols@ljmu.ac.uk).

## **Acknowledgements**

We are grateful to Uganda Wildlife Authority and Uganda National Council for Science and Technology for permission to carry out our research, and the Wardens of Queen Elizabeth National Park for logistical support. We thank F. Mwanguhya, S. Kyabulima, K. Mwesige, R. Businge, H. Marshall and E. Vitikainen for assistance in the field, and two anonymous reviewers for their helpful comments.

# 1 **Adjustment of costly extra-group paternity according to inbreeding risk in a** 2 **cooperative mammal**

3 **Abbreviated title:** Costs and benefits of extra-group paternity in banded mongooses

## 4 **Abstract**

5 Females of many animal species seek mating opportunities with multiple males, despite  
6 being able to obtain sufficient sperm to father their offspring from a single male. In animals that live  
7 in stable social groups, females often choose to mate outside their group resulting in extra-group  
8 paternity. One reason proposed to explain female choice for extra-group males is to obtain  
9 compatible genes, for example in order to avoid inbreeding depression in offspring. The benefits of  
10 such extra-group paternities could be substantial if they result in fitter, outbred offspring. However,  
11 avoiding inbreeding in this way could be costly for females, for example through retaliation by  
12 cuckolded males or through receiving aggression whilst prospecting for extra-group mating  
13 opportunities. We investigate the costs and benefits of extra-group paternity in the banded  
14 mongoose *Mungos mungo*, a cooperatively breeding mammal in which within-group mates are  
15 sometimes close relatives. We find that pups born to females that mate with extra-group males are  
16 more genetically heterozygous, are heavier and are more likely to survive to independence than  
17 pups born to females that mate within their group. However, extra-group matings also involve  
18 substantial costs as they occur during violent encounters that sometimes result in injury and death.  
19 This appears to lead female banded mongooses to adaptively adjust extra-group paternity levels  
20 according to the current risk of inbreeding associated with mating within the group. For group-living  
21 animals, the costs of inter-group interactions may help to explain variation in both inbreeding rates  
22 and extra-group paternity within and between species.

23 **Key words:** extra-group paternity, extra-pair paternity, mammal, mating system, inter-group  
24 interaction, warfare

25

26 **Lay summary**

27 Female banded mongooses risk their lives to mate with rivals during pack 'warfare'. Data from wild  
28 banded mongooses reveal that 18% of pups are fathered by males from rival packs. These pups are  
29 less likely to be inbred, are heavier and have higher survival chances than their within-pack  
30 counterparts. However, their mothers risk a lot to mate with extra-pack males; aggressive  
31 encounters between packs account for 20% of pup deaths and 12% of adult deaths.

32 **Introduction**

33 Females often choose to mate with multiple males despite being able to obtain sufficient  
34 sperm to fertilize their eggs from a single male. Why they do so is not immediately obvious and  
35 consequently has been a topic of much debate (Akçay & Roughgarden, 2007; Forstmeier et al., 2014).  
36 Among animals that live in stable groups, females often copulate with males outside their social unit  
37 (Griffith et al., 2002). Among birds, most of which are socially monogamous (Cockburn, 2006), extra-  
38 group paternity is known as extra-pair paternity (extra-group paternity when the group size is two),  
39 whilst among mammals, individuals tend to live in groups, so the term extra-group paternity is  
40 generally applied (Isvaran & Clutton-Brock, 2007).

41 Females can benefit from seeking multiple mates in two main ways. Firstly, females may  
42 obtain direct benefits from mating multiply. For example, the paternity uncertainty created through  
43 polyandrous mating can lead to an increase paternal care (Goldizen, 1987; Santos & Nakagawa, 2013)  
44 or a reduction in the probability of infanticide (Lukas & Huchard, 2014). Secondly, females may gain  
45 genetic benefits for their offspring through obtaining 'good genes' or 'compatible genes' from a male  
46 other than her social partner or the dominant male in her territory (Foerster et al., 2003). Good  
47 genes are those that may be associated with heritable traits related to male attractiveness,  
48 survivability or competitive ability (Forstmeier, et al., 2014). If females are mating for good genes,  
49 they may either select a mate with particularly advantageous traits, or may mate multiply as a form

50 of genetic bet-hedging (Fox & Rauter, 2003; Forstmeier, et al., 2014). Compatible genes are often  
51 thought to be those that lead to genetically heterozygous offspring, since heterozygosity reduces the  
52 likelihood of suffering from inbreeding depression (Hoffman et al., 2007). Females seeking  
53 compatibility should therefore attempt to mate with males that are genetically dissimilar to  
54 themselves. In accordance with this hypothesis, many studies have revealed that extra-pair or group  
55 mates are less related to females than their within-pair mates (Blomqvist et al., 2002; Foerster, et al.,  
56 2003; Brouwer et al., 2011; Arct et al., 2015), although not in every case; (Harrison et al., 2013; Hsu  
57 et al., 2015). It is also important to note that outbreeding depression is possible where strong local  
58 adaptation is present, hence females may not always be selected to maximize offspring  
59 heterozygosity. However, this appears to be relatively rare (Frankham et al., 2011).

60         The benefit of seeking compatible genes may be particularly important in species where  
61 potential mates are close relatives. In many cooperatively breeding species, high levels of natal  
62 philopatry mean that potential mates from within the group are often closely related (Koenig &  
63 Haydock, 2004). Here, extra-group paternity can be an important mechanism of inbreeding  
64 avoidance. For example, in splendid fairy-wrens *Malurus splendens* and superb fairy-wrens *Malurus*  
65 *cyaneus*, many social pairs are first order relatives. In these species, inbreeding is avoided through  
66 an exceptionally high rate of extra-group paternity (over 70%) (Koenig & Haydock, 2004). Similarly, in  
67 pilot whales *Globicephala melas* and killer whales *Orcinus orca*, both sexes are philopatric, leading to  
68 high within-group relatedness. Here, all mating appears to be extra-group (Amos et al., 1991; Pilot et  
69 al., 2010).

70         Whilst polyandrous mating can benefit a female, mating with males other than their social  
71 partner or the resident dominant male may come at a cost. In some species, high predation levels  
72 lead to constraints on prospecting for mates (Bennett & Faulkes, 2000). Studies have also shown  
73 that females who mate extra-group can have reduced paternal care for their offspring (Suter et al.,  
74 2009; García-Navas et al., 2013), or increased aggression from their social partner (McKibbin et al.,

75 2011; García-Navas, et al., 2013; Hoi et al., 2013). Females may also risk losing offspring if they are  
76 left unattended while seeking an extra-group mate (Hoffman, et al., 2007). In species where territory  
77 borders are defended aggressively, attempts to encounter other social groups can be particularly  
78 risky (Watts et al., 2006). If an aggressive interaction occurs, females or their offspring may be  
79 injured or killed and, even if receptive females are not targeted, the death of other group-members  
80 will lead to a reduction in group size which can in-turn impact on territory size and survival (Kokko et  
81 al., 2001).

82           Although the costs of extra-group paternity may be an important determinant of whether  
83 or not females seek extra-group matings, this possibility has received little attention (Forstmeier, et  
84 al., 2014). Here, we investigate the costs and benefits of extra-group paternity in a social mammal;  
85 the banded mongoose *Mungos mungo*. This species lives in large mixed sex groups of 5-40 adults  
86 (mean group size = 29) and has a polygynandrous mating system, with each group containing a 'core'  
87 of one to five dominant breeders of each sex, along with younger subordinates that breed  
88 occasionally (Cant et al., 2013). New groups are formed when a cohort of males from one natal  
89 group joins a cohort of females from another natal group; hence group-founders are closely related  
90 within each sex but unrelated between the sexes (Nichols et al., 2012). Although both males and  
91 females sometimes disperse from their natal groups, both sexes often remain philopatric. This, along  
92 with the death of group-founders, leads to a build-up of relatives in the group over time since the  
93 group was founded (Nichols, et al., 2012). By the time a group reaches 10 years old, the mean level  
94 of genetic relatedness between opposite-sex adult group-members is 0.25 (Nichols, et al., 2012).  
95 Consequently, females that breed within their natal group often mate with relatives including  
96 fathers and brothers (Nichols et al., 2014). Extra-group paternity could therefore be an important  
97 way in which inbreeding can be avoided in this species.

98           Banded mongoose groups generally breed three to four times per year (Cant, et al., 2013).  
99 Female group-members enter estrus together (within 7 days of each other) and each female is

100 guarded by a within-group male (Nichols et al., 2010). However, females are capable of refusing  
101 mating attempts and it does not appear to be possible for males to force female to mate (Cant,  
102 2000). Females are often able to escape their mate-guard to mate with other group-members (Cant,  
103 2000). Extra-group mating has been observed during inter-group encounters (Cant et al., 2002) but  
104 such mating is difficult to observe as it is often surreptitious and occurs in dense bushes.  
105 Nevertheless, extra-group paternity does occur in our study population, with extra-group males  
106 fathering 20% of pups (Nichols, et al., 2014). A previous study (Cant, et al., 2002) found that  
107 although 65% of inter-group encounters occur in areas of overlap between territories, both sexes  
108 are involved in initiating encounters by leading their group deep into neighboring territories: estrus  
109 females initiated 11% of inter-group encounters, whilst a further 24% were initiated by males (Cant,  
110 et al., 2002). This leads to a higher inter-group encounter rate during estrus (Cant, et al., 2002).  
111 During inter-group encounters, both resident and intruding females have been observed to mate  
112 extra-group (Cant et al., 2002). However, inter-group encounters are often violent and lead to injury  
113 and death, and may pose a risk to females or their offspring (Cant, et al., 2002).

114 A previous study (Nichols, et al., 2014) demonstrated that inbreeding is relatively common in  
115 the banded mongoose, with 14.3% of pups being moderately inbred ( $F = 0.125$ ) and 8% of pups  
116 being highly inbred (i.e. the product of father-daughter and full-sibling matings,  $F = 0.25$ ). Inbreeding  
117 appears to be influenced by female dispersal and mating patterns; the majority of pups (63.9%) are  
118 born to females breeding within their natal group, and these females often conceive to relatives,  
119 whilst females that mate-extra-group or disperse mate with non-relatives (Nichols, et al., 2014). The  
120 study also found that a significantly larger proportion of pups were fathered by extra-group males  
121 when females bred within their natal group in comparison to females that dispersed (Nichols, et al.,  
122 2014). This highlights extra-group paternity as a potentially important means by which females could  
123 reduce their probability of inbreeding.



124 Here, we extend this work by investigating the costs and benefits of extra-group mating for  
125 female banded mongooses. Specifically, we test 1) whether pups fathered by extra-group males are  
126 genetically more heterozygous or more competitive than pups fathered by males within the group; 2)  
127 whether engaging in or seeking extra-group copulations involves costs to females; 3) whether  
128 females are more likely to seek extra-group paternity when the risk of inbreeding within groups is  
129 high.

130

## 131 **Methods**

### 132 **Study site and life-history data collection**

133 Data were collected from a population of wild banded mongooses in Queen Elizabeth  
134 National Park, Uganda (0°12'S, 27°54'E) between 1997 and 2011. The climate is equatorial with little  
135 seasonal variation in temperature and two rainy seasons per year. Further details of habitat and  
136 climate are given elsewhere (Cant, et al., 2013). All individuals in the study population were  
137 habituated to the presence of human observers at 2 – 4 m. Groups were visited every 1 – 4 days to  
138 collect behavioral and life history data and are typically visited every day during oestrus, when inter-  
139 group interactions are most frequent. At each visit (lasting a minimum of 20 minutes), the  
140 composition of the group was recorded. Life-history information, such as births, deaths and dispersal  
141 events were recorded, and we knew accurate ages for the majority of the population. It was possible  
142 to distinguish death from dispersal as most dispersal events are induced through intense aggression  
143 from dominant group members (known as eviction) (Cant et al., 2001). Also, individuals disperse in  
144 single-sex cohorts and have never been observed to disperse alone, so the disappearance of a single  
145 individual with no prior signs of aggression was likely to be due to death (Cant, et al., 2001). Where  
146 known or heavily implied, we recorded the cause of death.

147 Encounters between neighboring groups (inter-group interactions; IGIs) were recorded *ad*  
148 *libitum*. Inter-group encounters are described in detail elsewhere (Cant, et al., 2002). In brief, when  
149 packs sight each other, they respond by standing erect and giving a distinctive, screeching call which  
150 alerts the rest of their pack to the presence of another group. When there are large size differences  
151 between the packs, the smaller group often flees. However, when groups are closely matched in size,  
152 individuals bunch together and approach the opposing group. Once groups are 20 – 30m apart, they  
153 rush forward and engage in fights and chases. Fights are highly aggressive, involving biting and  
154 scratching, often to the head and legs. Attacks occur within and between the sexes (i.e. are not  
155 purely intra-sexual). Occasionally, successful mating attempts have been observed to occur during  
156 these encounters. A video example of an inter-group interaction, including both fighting and mating  
157 is included in the supplementary material (SI1).

158 One or two individuals in each group were fitted with a radio collar (Sirtrack Ltd., New  
159 Zealand). Individuals could be identified in the field by either color coded plastic collars or through  
160 unique patterns shaved or dyed in their fur on their backs. Shavings, collars and dye patterns were  
161 maintained through regular trapping (every 3 – 6 months). Individuals were trapped using baited  
162 cage traps, and were anaesthetized using isoflurane or using intramuscular injections of 1mg/kg of  
163 ketamine and 0.8mg/kg of medetomidine, followed by an injection of 0.8mg/kg of atapamezol after  
164 handling (further details are given elsewhere: Hodge 2007, Jordan et al. 2010). Pups were first  
165 trapped at age 30 – 50 days. On first capture, permanent identification was made possible using  
166 either a uniquely coded tattoo or a pit tag, and a ~2 mm tail tip skin sample was collected for genetic  
167 analysis (Nichols, et al., 2010). This trapping protocol was used over 6000 times during the course of  
168 study without any individuals dying or becoming noticeably sick. This research was carried out under  
169 license from the Uganda National Council for Science and Technology and all procedures were  
170 approved by the Uganda Wildlife Authority.

## 171 **Genetic analysis**

172 DNA was extracted from 1534 tail-tips by lysis with ProteinaseK, followed by phenol-  
173 chloroform purification (Sambrook et al., 1989) or using DNA extraction kits (Qiagen® Tissue and  
174 Blood Kit). Samples were genotyped at up to 20 microsatellite loci, isolated from a variety of  
175 carnivore species, including the banded mongoose (Table S1). Genotyping was conducted following  
176 (Nichols, et al., 2010) or (post-2010) using multiplex PCRs (Qiagen® Multiplex PCR Kit, UK) with  
177 fluorescent-labelled forward primers and were visualized through fragment size analysis on an ABI  
178 3730 DNA Analyzer. PCR conditions followed the Qiagen® Multiplex PCR Kit recommendations (but  
179 were conducted in 12µl reactions), with an annealing temperature of 57°C.

180 Values of pairwise relatedness were calculated following Lynch & Ritland (1999), and  
181 heterozygosity was calculated using HL following Aparicio et al. (2006). Parentage analysis was  
182 conducted using Cervus, version 3.0 (Marshall et al., 1998). As maternity could be narrowed down to  
183 a small number of females (mean = 4.3 per pup), maternities were assigned first. Several female  
184 group-members often gave birth in synchrony, and the subsequent litter is raised communally (Cant,  
185 et al., 2013). As a consequence, all visibly pregnant females present in the group at the time of litter  
186 birth were included as candidate mothers to all pups born in the communal litter. For individuals  
187 where maternity was assigned at  $\geq 95\%$  confidence, paternity was then assigned assuming the  
188 maternity to be correct. All males in the study population over 1 year old at litter conception (60  
189 days before birth) were included as candidate fathers (mean = 72.5 per pup). In order to establish  
190 the confidence level of each assignment, Cervus conducts simulations of parentage assignment.  
191 Simulations took into account the relatedness structure of the banded mongoose population, with  
192 all candidate mothers being related to the real mother by 0.25, and 10% of candidate fathers being  
193 related to the real father by 0.2. Of the 1131 pups included in parentage analysis, maternities were  
194 assigned to 906 pups at  $\geq 95\%$  confidence and paternities were assigned to 629 of these pups at  $\geq 95\%$   
195 confidence (equivalent to  $\geq 90\%$  confidence after taking into account the probability of mis-assigning  
196 the maternity).

## 197 **Statistical analyses**

198 All statistical analyses were carried out using R 3.0.1 using either the lme4 or glmmADMB  
199 packages (Fournier et al., 2011; Bates et al., 2013). General linear mixed effect models (LMMs) and  
200 generalized linear mixed effect models (GLMMs) were used to control for repeated measures within  
201 years, social groups, breeding attempts, and individuals (where appropriate). Response variables  
202 followed normal, binomial, or Poisson distributions and were fitted in models with identity, logit,  
203 and log link functions, respectively. When data was zero-inflated, models were fitted using the  
204 glmmADMB package (Fournier et al., 2011) and model comparisons were made using likelihood ratio  
205 tests. Full models containing all possible explanatory variables were constructed and were simplified  
206 by stepwise model simplification; variables with the lowest explanatory power were sequentially  
207 dropped from the model until only those variables explaining significant variation ( $p < 0.05$ )  
208 remained. All dropped variables were then put back into the minimal model one at a time to  
209 determine their level of non-significance. As some data (such as body weight) is only available from a  
210 subset of individuals, models varied in their sample sizes. In each model, we used the maximum  
211 sample size available to us. Details of the models fitted, including sample sizes, are included in Tables  
212 1-4, 6 and 7.

## 213 **Results**

### 214 *1. Are pups fathered by extra-group males more competitive than within-group pups?*

215 Parentage analysis uncovered 112 cases of extra-group paternity (17.8% of the 629 pups  
216 assigned a father). Pups that were the product of extra-group paternity were on average more  
217 genetically heterozygous than pups that are the product of within-group matings (LMM:  $\chi^2_{(1)} = 5.69$ ,  
218  $p = 0.017$ , Table 1, Figure 1a). This is in accordance with previous work, which found that females  
219 mating with extra-group males were less related to their mates than females that mated within-  
220 group (Nichols, et al., 2014).

221 Pups fathered by extra-group males were significantly heavier at emergence from the natal  
222 den (30-40 days old) than pups fathered by within-group males (LMM:  $\chi^2_{(1)} = 5.28$ ,  $p = 0.022$ , Table 2,  
223 Figure 1b). Furthermore, pups fathered by extra-group males were significantly more likely to  
224 survive to nutritional independence (90 days) than within-group pups (LMM:  $\chi^2_{(1)} = 5.43$ ,  $p = 0.020$ ,  
225 Table 3, Figure 1c). However, there was no significant impact of extra-group paternity on weight as a  
226 yearling (LMM:  $\chi^2_{(1)} = 2.53$ ,  $p = 0.11$ , Table 2) or on survival to one year (LMM:  $\chi^2_{(1)} = 0.05$ ,  $p = 0.82$ ,  
227 Table 3).

## 228 *2. Are there costs to females of extra-group mating?*

229 Previous behavioral observations indicate that extra-group mating attempts primarily occur  
230 during aggressive encounters between neighboring groups (Cant, et al., 2002). In accordance with  
231 this, we found that extra-group paternity was significantly more likely to be assigned in communal  
232 litters when an inter-group encounter was observed during the estrus period (LMM:  $\chi^2_{(1)} = 4.62$ ,  $p =$   
233  $0.032$ , Table 4, Figure 2a).

234 To investigate the potential costs of engaging in inter-group interactions, we quantified the  
235 proportion of individuals that were known to die due to inter-group interactions. We found that, of  
236 the 687 individuals where cause of death is known (or heavily implied), a substantial proportion  
237 (15%) died during or following injury from inter-group encounters (Table 5). Pups (under 90 days)  
238 appear to be particularly vulnerable during inter-group encounters; inter-group aggression accounts  
239 for 20% of pup deaths, compared to 12% of adult deaths, a significant difference (pups: 76/382,  
240 adults: 26/210,  $\chi^2_{(1)} = 4.85$ ,  $p = 0.028$ ). However, there was no significant difference in the  
241 proportions of adult male and female (over 1 year old) deaths in inter-group interactions (males:  
242 19/124, females: 7/86,  $\chi^2_{(1)} = 1.80$ ,  $p = 0.180$ ). Together, this data suggests that females can suffer  
243 costs to engaging in inter-group encounters, including death, the loss of pups from previous litters  
244 and a reduction in group size which may in-turn impact on territory size and survival.

245 3. Are females more likely to mate extra-group when the risk of inbreeding within groups is high?

246           Given the costs involved in extra-group mating, we predicted that females should seek  
247 mating opportunities outside their own group when there is a high risk of inbreeding by mating with  
248 within-group males. In support of this prediction, the probability of finding extra-group paternity in a  
249 communal litter was higher in older groups (LMM:  $\chi^2_{(1)} = 9.57$ ,  $p = 0.0020$ , Table 6, Figure 2b), which  
250 contain more relatives (Nichols, et al., 2012). Once group-age had been taken into account, there  
251 was a non-significant trend for higher levels of extra-group paternity in groups with higher mean  
252 levels of relatedness between opposite sex adult group members (LMM:  $\chi^2_{(1)} = 3.02$ ,  $p = 0.082$ ,  
253 Table7).

254           Early-life mortality resulting from inbreeding depression can potentially bias estimates extra-  
255 group paternity frequency (Reid et al., 2014). If offspring with extra-group fathers are less inbred and  
256 hence have higher survival chances than within-group offspring, mortality prior to genetic sampling  
257 could result in a spurious relationship between the probability of finding extra-group offspring and  
258 inbreeding risk. As we found evidence of lower early-life mortality in extra-group banded mongoose  
259 pups, it is likely that extra-group pups also have lower mortality prior to emergence from the den  
260 (and genetic sampling), making such biases likely in our system. The potential bias can be assessed  
261 by simulations, which take into account the probability of an offspring dying prior to genetic  
262 sampling (Reid, et al., 2014). Unfortunately, in the banded mongoose, it is not possible to estimate  
263 the proportion of pups that die prior to sampling as females give birth in inaccessible underground  
264 dens and pups do not emerge for ~30 days, so litter-size at birth is unknown (Cant, et al., 2013).  
265 Instead, we sought to investigate whether females mate extra-group when they are at risk of  
266 inbreeding within groups is high using behavioral records of inter-group interactions, which are not  
267 subject to biases in genetic sampling. We found that inter-group encounters were significantly more  
268 likely to occur during estrus in older groups (GLMM:  $\chi^2_{(1)} = 13.66$ ,  $p = 0.0002$ , Figure 3, Table 7) which  
269 contain more opposite-sex relatives (Nichols, et al., 2012). However, there was no additional impact

270 of average male-female relatedness on the numbers of inter-group interactions that occur (GLMM:  
271  $\chi^2_{(1)} = 0.004$ ,  $p = 0.95$ , Table 7).

272

## 273 **Discussion**

274 We found evidence of substantial benefits to females of mating with males from a different  
275 social group. Firstly, pups fathered by extra-group males had higher levels of genetic heterozygosity  
276 than within-group pups. This is probably because extra-group mates are on average less related to  
277 the mother than within-group mates (Nichols, et al., 2014), and hence extra-group pups are outbred  
278 in comparison to their within-group counterparts. Furthermore, we found that pups fathered by  
279 extra-group males are heavier at emergence from the den (30-40 days) than those fathered by  
280 within-group males. This early life weight advantage may have an important influence on survival  
281 because heavier pups are at an advantage when competing with their littermates for access to  
282 carers (Hodge et al., 2009). Accordingly, pups fathered by extra-group males were more likely to  
283 survive until nutritional independence (90 days) than pups fathered by within-group males. However,  
284 we did not find effects of extra-group paternity on weight and survival among yearlings, suggesting  
285 that the costs of inbreeding depression may be particularly high in early life. This result is in  
286 accordance with a study on the closely related meerkat, which found evidence for inbreeding  
287 depression on a range of early-life traits including pup mass at emergence and juvenile survival  
288 (Nielsen et al., 2012).

289 Although mating with extra-group males can be advantageous to banded mongoose females,  
290 these matings may come at a cost. Extra-group matings occurred during violent inter-group  
291 encounters, which account for a high proportion of adult and pup mortality (12% and 20% of known  
292 causes of death respectively, including females of breeding age). Females may therefore suffer costs  
293 to engaging in inter-group encounters including death, the loss of pups from previous litters and a

294 reduction in group size which can in-turn impact on territory size and survival (Cant, et al., 2002;  
295 Furrer et al., 2011). Furthermore, as banded mongooses breed regularly, females are pregnant for  
296 around 30% of each year ( $108 \pm 4.8$  days per year,  $N = 199$  females aged over 1 year; H. Marshall,  
297 unpublished data), so any injury is likely to have direct fitness consequences. Aggressive inter-group  
298 interactions have been observed in other group-living carnivores and primates (Gray wolves *Canis*  
299 *lupus* (Cassidy, 2013), Ethiopian wolves *Canis simensis* (Sillero-Zubiri & Macdonald, 1998), African  
300 lions *Panthera leo* (Mosser & Packer, 2009), spotted hyenas *Crocuta crocuta* (Boydston et al., 2001)  
301 common marmosets *Callithrix jacchus* (Lazaro-Perea, 2001), chimpanzees *Pan troglodytes*, and  
302 humans *Homo sapiens* (Wrangham et al., 2006)). In the majority of these species, aggressive  
303 interactions rarely involve matings, and instead appear to be related to inter-group competition over  
304 territory; killing or injuring rival group-members reduces the competitive ability of rival groups and  
305 hence increases the aggressors ability to acquire territory (Wrangham & Glowacki, 2012). However,  
306 in a subset of these species, extra-group matings have been observed (common marmosets (Lazaro-  
307 Perea, 2001)), or aggression towards opposite-sex intruders is rare (Ethiopian wolves (Sillero-Zubiri  
308 & Macdonald, 1998), spotted hyenas (Boydston, et al., 2001)), suggesting that individuals may use  
309 aggressive inter-group interactions as an opportunity to prospect for mating opportunities. In the  
310 banded mongoose, territory gain is likely to be important in determining the frequency of aggressive  
311 inter-group interactions (Cant, et al., 2002; Furrer, et al., 2011). However, the relationship between  
312 inter-group interactions and extra-group paternity strongly suggests that access to mating  
313 opportunities is also important.

314 In species that have aggressive inter-group encounters, deaths are often biased towards  
315 adult males. For example across seven human subsistence farming societies, the median percentage  
316 of deaths due to inter-group warfare was 28.5% for males and 6.1% for females (Wrangham, et al.,  
317 2006). Similarly, among chimpanzee societies, adult males are > 6 times more likely to be the victims  
318 of lethal inter-group aggression than females (Wrangham, et al., 2006). In contrast, for the banded  
319 mongoose, we found no significant differences between the proportion of adult males and females



320 dying during inter-group encounters. This could be because inter-group encounters occur when  
321 entire groups meet, rather than on single-sex patrols as in chimpanzees (Wrangham & Glowacki,  
322 2012), hence females have little choice but to participate. Alternatively, these patterns may be due  
323 patterns of philopatry (Kitchen & Beehner, 2007). In contrast to chimpanzees and humans (where  
324 females disperse) in banded mongooses both sexes can remain in their natal group for their entire  
325 lives and hence have high relatedness to the rest of their group (Nichols, et al., 2012). Males and  
326 females may therefore gain equally from maintaining territory size and from reducing the group-size  
327 of rival groups.

328           In the banded mongoose, we found that the frequency of extra-group paternity increased  
329 with group age. This is consistent with the idea that estrus females may adaptively seek extra-group  
330 paternity when the probability of mating with a relative within the group is high (older groups  
331 contain more opposite-sex relatives (Nichols, et al., 2012)). Higher levels of inter-group interactions  
332 during estrus in older groups further support the idea that this relationship is due to variation in  
333 mating frequency, rather than being due to biases in early-life mortality (as suggested by Reid, et al.  
334 (2014)). Although group age had significant positive effect on the frequency of inter-group  
335 interactions during estrus and on the probability of observing extra-group pups, mean male-female  
336 relatedness within the group did not. It is possible that group age is a better measure of inbreeding  
337 risk than mean relatedness as mean relatedness does not take within-group variance in relatedness  
338 into account, which could be important in governing mating decisions. Alternatively, banded  
339 mongooses may be unable to assess genetic relatedness directly, for example through scent cues  
340 (Mateo & Johnston, 2000). Instead, they may use a simple rule governing when to mate extra-group,  
341 which is more closely associated with group age than it is to mean male-female relatedness. For  
342 example, female group founders may change their mating behavior over time as the number of  
343 related males (e.g. their sons and nephews) in the group increases. Natal females, on the other hand,  
344 may always assume that they are related to male group-members, and will mate extra-group where  
345 possible. Therefore, the proportion of females attempting to breed extra-group may increase over

346 time since group formation due to an increase in the proportion of natal females, and changes in the  
347 behavior of group-founding females. Mechanisms of kin recognition will be the subject of future  
348 study. Although our results are consistent with adaptive female choice for non-relatives, we cannot  
349 currently eliminate alternative explanations. For example, although females cannot be forced to  
350 mate (Cant, 2000), they may be coerced into mating through threat of aggression during inter-group  
351 interactions. This may explain why a small proportion of females mate extra-group even after  
352 dispersal from their natal group (Nichols, et al., 2014). However, on average, females appear to  
353 benefit from extra-group matings through producing pups that are more genetically heterozygous,  
354 heavier and are more likely to survive until independence, suggesting that females may mate  
355 willingly with extra-group males.

356 Adaptive female mate-choice in order to receive compatible genes has been proposed in a  
357 number of vertebrate species, such as Antarctic fur seals *Arctocephalus gazella* (Hoffman, et al.,  
358 2007) alpine marmots *Marmota marmota* (Cohas et al., 2008), European badgers *Meles meles*  
359 (Annavi et al., 2014), western sandpipers *Calidris mauri*, common sandpipers *Actitis hypoleuca* and  
360 Kentish plovers *Charadrius alexandrinus* (Blomqvist, et al., 2002). While there is strong evidence of  
361 adaptive mate choice for good or compatible genes in some cases, broader-scale patterns across  
362 birds and mammals are not well supported (Griffith, et al., 2002; Akçay & Roughgarden, 2007; Hsu,  
363 et al., 2015). For example, a meta-analysis by Akçay & Roughgarden (2007) found that fewer than  
364 half of studies supported adaptive extra-pair paternity to gain good or compatible genes. This  
365 suggests that there may be additional factors influencing the distribution of extra-group paternity  
366 across species. For example, ecological or social constraints on mating opportunities may prevent  
367 females from mating extra-group and hence mask the effect of good or compatible genes (Akçay &  
368 Roughgarden, 2007), or methodological differences between studies may impact on their ability to  
369 detect an effect (Arct, et al., 2015). Alternatively, compatible genes may be particularly important in  
370 a subset of species, such as those where inbreeding is particularly likely to occur if females mate  
371 within their social system, as is the case in the banded mongoose.

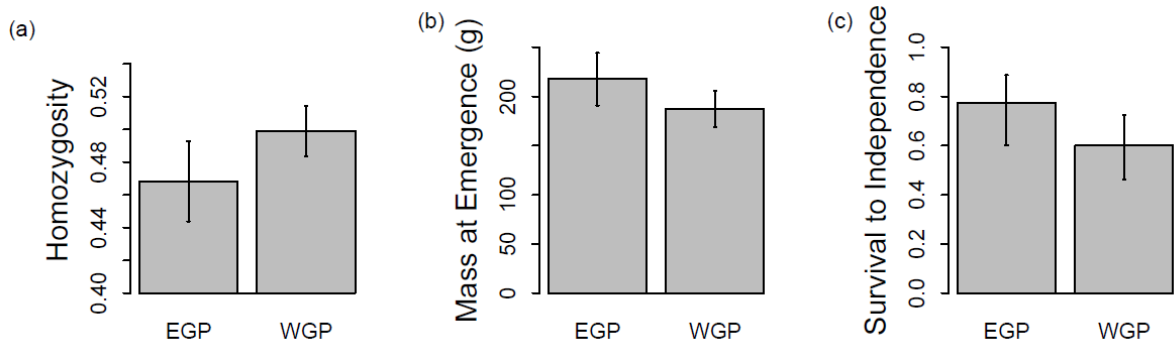
## 372 **Conclusion**

373           We show that female banded mongooses obtain genetic benefits from mating with extra-  
374 group males. Pups with extra-group fathers are more genetically heterozygous, heavier, and are  
375 have higher survival rates than pups produced by within-group males. However, extra-group mating  
376 comes at a cost. Inter-group encounters, where extra-group mating takes place, are highly  
377 aggressive and result in high levels of mortality, especially for pups. Females engaging in inter-group  
378 encounters therefore risk the loss of dependent pups, in addition to personal injury or death. As a  
379 consequence, females appear to strategically adapt their frequency of extra-group paternity  
380 according to current inbreeding risk, with extra-group paternity being more likely to be found in  
381 older social groups, which contain more relatives. Higher levels of inter-group interactions during  
382 estrus in older groups support the idea that this relationship is due to variation in mating frequency,  
383 rather than simply on biases in early-life mortality. This study highlights the potential importance of  
384 the costs of extra-group paternity in determining the frequency of extra-group or pair paternity,  
385 which are rarely considered. The costs of obtaining extra-group mating partners may also contribute  
386 towards explaining variance in both inbreeding rates and extra-group paternity rates between  
387 species.

## 388 **Data Accessibility**

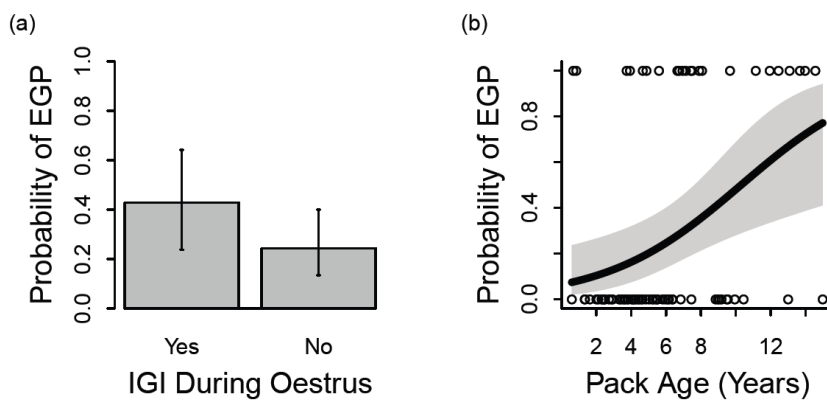
389           Microsatellite sequences are available from Genbank: accession numbers can be found in Table S2.1.

390



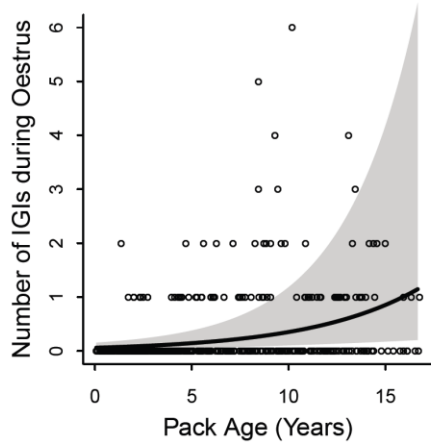
391

392 **Figure 1.** Effects of EGP on (a) offspring homozygosity, (b) offspring body mass at emergence (30 –  
 393 40 days), and (c) offspring survival to independence (90 days). Bars and confidence intervals show  
 394 predicted means and standard errors, respectively (while controlling for a significant effect of rainfall  
 395 on survival to emergence).



396

397 **Figure 2.** The effects of (a) an inter-group interaction (IGI) occurring during group estrus and (b) pack  
 398 age (years since the group was founded) on the probability of extra-group paternity (EGP) occurring  
 399 within a communal litter. Figures show predicted means and standard errors from two GLMMs.



400

401 **Figure 3.** The impact of pack age (years since the group was founded) on the number of inter-group  
402 interactions (IGIs) occurring during estrus ( $60 \pm 5$  days before birth). Points show raw data while the  
403 line and shaded area show the predicted trend with confidence intervals from a GLMM while  
404 controlling for zero-inflation and the number of inter-group interactions observed in a comparative  
405 time period after estrus ( $40 \pm 5$  days before birth).

406

407

408 Table 1. A LMM investigating whether extra-group males produce less homozygous pups than  
 409 within-group males.

<b>Factors affecting offspring homozygosity</b>			
Model Term	Average effect ±SE	Wald Statistic ( $\chi^2$ )	<i>P</i>
<b>Extra-group paternity</b>	<b>-0.031 ± 0.013</b>	<b>5.69</b>	<b>0.017</b>
Constant	0.50 ± 0.0078		
Random effects: group, litter, mother's ID, father's ID and year. N = 629 pups from 196 communal litters in 16 groups over 15 years, produced by 126 mothers and 138 fathers.			

410

411 Pup homozygosity was fitted as a normally distributed response variable with extra-group paternity  
 412 as an explanatory factor.

413

Table 2. LMMs investigating whether extra-group pups are heavier at emergence from the natal den (at 30-40 days of age) than within-group pups.

Model Term	Factors affecting mean weight at emergence (aged 30-40 days)		Wald		Factors affecting mean weight at emergence (aged 350-380 days)		Wald Statistic ( $\chi^2$ )
	Average effect $\pm$ SE		Statistic ( $\chi^2$ )	<i>P</i>	Average effect $\pm$ SE	Statistic ( $\chi^2$ )	
Extra-group paternity	<b>30.03</b> $\pm$ <b>12.75</b>		<b>5.28</b>	<b>0.022</b>	53.87 $\pm$ 32.69		2.0
Number of pups in litter	-0.63 $\pm$ 1.87		0.089	0.77	0.55 $\pm$ 4.61		0.0
Rainfall (mm)	4.23 $\pm$ 3.91		1.10	0.29	<b>-26.56</b> $\pm$ <b>8.01</b>		<b>9.0</b>
Group size	-1.28 $\pm$ 1.05		0.49	0.48	4.80 $\pm$ 2.90		2.0
Mother's age	-0.17 $\pm$ 0.23		0.50	0.48	0.86 $\pm$ 0.64		1.0
Constant	187.53 $\pm$ 9.01				1258.11 $\pm$ 55.33		

Random effects: pack, n = 104 pups from 45 communal litters over 11 years n = 121 yearlings from 64 communal  
year, litter ID, in 6 packs, with 42 fathers and 34 mothers. in 7 packs, with 62 fathers and 54 mothers  
mother's ID, father's  
ID

---

Measurements of body mass (grams) were fitted as a normally distributed response variables and whether or not the  
male was fitted as the main explanatory variable of interest in both models. The following were controlled for by fitting  
variables: the number of pups in the communal litter, the size of the social group (number of individuals over 1 year old)  
(mean rainfall in mm in 30 days prior to birth) and the mother's age at pup birth (months).



Table 3. GLMMs investigating whether extra-group pups are more likely to survive to nutritional independence (90 days) than group pups.

Model Term	Factors affecting survival to nutritional independence (90 days)			Factors affecting survival to 1 year		
	Average effect ±SE	Wald Statistic ( $\chi^2$ )	<i>P</i>	Average effect ±SE	Wald Statistic ( $\chi^2$ )	<i>P</i>
Extra-group paternity	<b>0.83 ± 0.38</b>	<b>5.43</b>	<b>0.020</b>	0.09 ± 0.49	0.00	0.96
Number of pups in litter	-0.022 ± 0.056	0.15	0.69	-0.08 ± 0.05	2.10	0.15
Rainfall (mm)	<b>0.30 ± 0.12</b>	<b>7.79</b>	<b>0.0052</b>	0.16 ± 0.11	2.10	0.15
Group size	-0.029 ± 0.031	0.86	0.35	-0.01 ± 0.02	0.00	0.96
Mother's age	0.0054 ± 0.0064	0.72	0.40	0.01 ± 0.01	0.00	0.96
Constant	-0.30 ± 0.38			0.64 ± 0.25		

---

Random effects: pack, n = 479 pups from 153 communal litters in 12 packs n = 272 pups from 120 communal litters  
year, litter ID, over 13 years, with 121 fathers and 100 mothers. 13 years, with 95 fathers and 77 mothers  
mother's ID, father's  
ID

---

Whether or not pups survived (1 = survived, 0 = did not survive) was fitted as a binomial response variable and whether an extra-group male was fitted as the main explanatory variable of interest in both models. The following were controlled explanatory variables: the number of pups in the communal litter, the size of the social group (number of individuals), rainfall (mean rainfall in mm in 30 days prior to birth) and the mother's age at pup birth (months).

Table 4. A GLMM investigating whether extra-group paternity is more likely to occur after inter-group encounters.

<b>Factors influencing the probability of extra-group paternity</b>			
Model Term	Average effect ±SE	Wald Statistic ( $\chi^2$ )	<i>P</i>
<b>Inter-group encounter</b>	<b>0.84 ± 0.39</b>	4.62	<b>0.032</b>
Constant	-1.14 ± 0.36		
Random effects: pack and year	n = 183 litters, 15 packs, 12 years		

Whether or not extra-group paternity was observed in a communal litter was included as a binomial response variable, and whether or not an inter-group encounter was observed during the estrus period ( $60 \pm 5$  days prior to birth of the communal litter) was included as an explanatory variable.

Table 5. Causes of death for 1808 banded mongooses, including 1103 pups (90 days and under) and 705 juveniles and adults.

<b>Cause of death</b>	<b>Number of individuals over 90 days old</b>	<b>% known</b>	<b>Number of pups (under 90 days old)</b>	<b>% known</b>
<b>Inter-group interaction (IGI)</b>	<b>30</b>	<b>10%</b>	<b>76</b>	<b>20%</b>
Age/sickness/generally weak	71	23%	48	13%
predated	155	51%	200	52%
Human induced	46	15%	10	3%
Eviction	2	<1%	N/A	N/A
Giving birth	1	<1%	N/A	N/A
Abandoned/kidnapped	N/A	N/A	18	5%
Within-group infanticide	N/A	N/A	30	8%
unknown	400		721	
Total known	305		382	
Total	705		1103	

Table 6. A GLMM investigating whether extra-group paternity is more likely to occur within a communal litter when the risk of inbreeding within a group is high (in older packs and when the mean relatedness between opposite-sex adults is high).

<b>Factors affecting probability of extra-group paternity within litter</b>				
Model Term	Average effect		Wald	<i>P</i>
	±SE		Statistic ( $\chi^2$ )	
<b>Number of (assigned) pups</b>	<b>0.21</b>	<b>± 0.10</b>	<b>4.61</b>	<b>0.032</b>
<b>Pack age (years)</b>	<b>0.26</b>	<b>0.09</b>	<b>9.57</b>	<b>0.0020</b>
Mean male-female relatedness	8.36	± 4.87	3.02	0.082
Constant	-3.69	± 0.95		
Random effects: pack, year	n = 78 communal litters from 11 social groups over 12 years			

Whether or not extra-group paternity was detected in a litter was fitted as a binomial response variable (0 = no extra-group paternity, 1 = at least one extra-group pup). Pack age (years since the group was founded) and the mean level of relatedness between adult male and female group-members (aged at least 1 year) were fitted as explanatory variables. It may be particularly difficult to detect whether or not extra-group paternity has occurred in a litter when a small proportion of pups have been genotyped and/or assigned paternity. To reduce the probability of this affecting the results, this analysis was limited to litters where at least 50% of pups were genotyped and assigned paternity (78 out of possible 189 communal litters) and for the remaining litters, the number of assigned pups was included as an explanatory variable in the model.

Table 7. A GLMM investigating whether inter-group interactions during pack estrus are more likely to occur within a communal litter when the risk of inbreeding within a group is high (in older packs and when the mean relatedness between opposite-sex adults is high).

<b>Factors affecting probability of extra-group paternity within litter</b>				
Model Term	Average effect ±SE		Deviance	<i>P</i>
<b>IGI count outside of estrus</b>	<b>0.24</b>	<b>0.09</b>	<b>6.54</b>	<b>0.011</b>
<b>Pack age (years)</b>	<b>0.16</b>	<b>0.05</b>	<b>13.66</b>	<b>0.0002</b>
Mean male-female relatedness	-0.11	1.52	0.004	0.95
Constant	-2.80	± 0.45		
Random effects: pack, year	n = 371 litters from 17 social groups over 17 years			

## References

- Akçay, E., & Roughgarden, J. 2007. Extra-pair paternity in birds: review of the genetic benefits. *Evolutionary Ecology Research*. 9: 855-868.
- Amos, B., Barrett, J., & Dover, G. A. 1991. Breeding behaviour of pilot whales revealed by DNA fingerprinting. *Heredity*. 67: 49-55.
- Annavi, G., Newman, C., Dugdale, H. L., Buesching, C. D., Sin, Y. W., Burke, T., & Macdonald, D. W. 2014. Neighbouring-group composition and within-group relatedness drive extra-group paternity rate in the European badger (*Meles meles*). *Journal of Evolutionary Biology*. 27: 2191-2203.
- Aparicio, J. M., Ortego, J., & Cordero, P. J. 2006. What should we weigh to estimate heterozygosity, alleles or loci? *Molecular Ecology*. 15: 4659-4665.
- Arct, A., Drobniak, S. M., & Cichoń, M. 2015. Genetic similarity between mates predicts extrapair paternity—a meta-analysis of bird studies. *Behavioral Ecology*.
- Bates, D., Maechler, M. B., B., & Walker, S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. <http://CRAN.R-project.org/package=lme4>.
- Bennett, N. C., & Faulkes, C. G. 2000. *African Mole-Rats: Ecology and Eusociality*. Cambridge University Press, UK.
- Blomqvist, D., Andersson, M., Küpper, C., Cuthill, I. C., Kis, J., Lanctot, R. B., Sandercock, B. K., Székely, T., Wallander, J., & Kempenaersq, B. 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature*. 419: 613-615.
- Boydston, E. E., Morelli, T. L., & Holekamp, K. E. 2001. Sex Differences in Territorial Behavior Exhibited by the Spotted Hyena (*Hyaenidae*, *Crocuta crocuta*). *Ethology*. 107: 369-385.
- Brouwer, L., van de Pol, M., Atema, E., & Cockburn, A. 2011. Strategic promiscuity helps avoid inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric. *Molecular Ecology*. 20: 4796-4807.

- Cant, M. A. 2000. Social control of reproduction in banded mongooses. *Animal Behaviour*. 59: 147-158.
- Cant, M. A., Otali, E., & Mwanguhya, F. 2001. Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of the Zoological Society of London*. 254: 155-162.
- Cant, M. A., Otali, E., & Mwanguhya, F. 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology*. 108: 541-555.
- Cant, M. A., Vitikainen, E., & Nichols, H. J. 2013. Demography and social evolution of banded mongooses. *Advances in the Study of Behavior*. 45: 407-445.
- Cassidy, K. A. 2013. Group composition effects on inter-pack aggressive interactions of gray wolves in Yellowstone National Park. University of Minnesota.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London. Series B, Biological Sciences*. 273: 1375-1383.
- Cohas, A., Yoccoz, N. G., Bonenfant, C., Goossens, B., Genton, C., Galan, M., & Allainé, D. 2008. The genetic similarity between pair members influences the frequency of extrapair paternity in alpine marmots. *Animal Behaviour*. 76: 87-95.
- Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. T., & Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature*. 425: 714-717.
- Forstmeier, W., Nakagawa, S., Griffith, S. C., & Kempenaers, B. 2014. Female extra-pair mating: adaptation or genetic constraint? *Trends in Ecology & Evolution*. 29: 456-464.
- Fournier, D. A., Skaug, H. J., Ancheta, J., Iannelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., & Sibert, J. 2011. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*. 27: 233-249.
- Fox, C. W., & Rauter, C. M. 2003. Bet-hedging and the evolution of multiple mating. *Evolutionary Ecology Research*. 5: 273-286.



- Frankham, R., Ballou, J. D., Eldridge, M. D. B., Lacy, R. C., Ralls, K., Dudash, M. R., & Fenster, C. B. 2011. Predicting the Probability of Outbreeding Depression. *Conservation Biology*. 25: 465-475.
- Furrer, R. D., Kyabulima, S., Willems, E. P., Cant, M. A., & Manser, M. B. 2011. Location and group size influence decisions in simulated intergroup encounters in banded mongooses. *Behavioral Ecology*. 22: 493-500.
- García-Navas, V., Ortego, J., Ferrer, E. S., & Sanz, J. J. 2013. Feathers, suspicions, and infidelities: an experimental study on parental care and certainty of paternity in the blue tit. *Biological Journal of the Linnean Society*. 109: 552-561.
- Goldizen, A. W. 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*. 20: 99-109.
- Griffith, S. C., Owens, I. P. F., & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*. 11: 2195-2212.
- Harrison, X. A., York, J. E., Cram, D. L., & Young, A. J. 2013. Extra-group mating increases inbreeding risk in a cooperatively breeding bird. *Molecular Ecology*. 22: 5700-5715.
- Hodge, S. J., Bell, M. B. V., Mwanguhya, F., Kyabulima, S., Waldick, R. C., & Russell, A. F. 2009. Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behavioral Ecology*. 20: 729-735.
- Hoffman, J. I., Forcada, J., Trathan, P. N., & Amos, W. 2007. Female fur seals show active choice for males that are heterozygous and unrelated. *Nature*. 445: 912-914.
- Hoi, H., Krištofík, J., & Darolová, A. 2013. Experimentally Simulating Paternity Uncertainty: Immediate and Long-Term Responses of Male and Female Reed Warblers *Acrocephalus scirpaceus*. *PLoS ONE*. 8: e62541.
- Hsu, Y.-H., Schroeder, J., Winney, I., Burke, T., & Nakagawa, S. 2015. Are extra-pair males different from cuckolded males? A case study and a meta-analytic examination. *Molecular Ecology*. 24: 1558-1571.

- Isvaran, K., & Clutton-Brock, T. H. 2007. Ecological correlates of extra-group paternity in mammals. *Proceedings of the Royal Society of London. Series B, Biological Sciences*. 274: 219-224.
- Kitchen, D. M., & Beehner, J. C. 2007. Factors Affecting Individual Participation in Group-Level Aggression among Non-Human Primates. *Behaviour*. 144: 1551-1581.
- Koenig, W., & Haydock, J. 2004. Incest and incest avoidance. In: W. Koenig and J. Dickinson (Editors.). *Ecology and Evolution of Cooperative Breeding in Birds*. (pp. 142-156). Cambridge: Cambridge University Press.
- Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London. Series B, Biological Sciences*. 268: 187-196.
- Lazaro-Perea, C. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Animal Behaviour*. 62: 11-21.
- Lukas, D., & Huchard, E. 2014. The evolution of infanticide by males in mammalian societies. *Science*. 346: 841-844.
- Lynch, M., & Ritland, K. 1999. Estimation of pairwise relatedness with molecular markers. *Genetics*. 152: 1753-1766.
- Marshall, T. C., Slate, J. B. K. E., Kruuk, L. E. B., & Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*. 7: 639-655.
- Mateo, J. L., & Johnston, R. E. 2000. Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. *Proceedings of the Royal Society of London. Series B, Biological Sciences*. 267: 695-700.
- McKibbin, W. F., Starratt, V. G., Shackelford, T. K., & Gotez, A. T. 2011. Percieved risk of female infidelity moderates the relationship between objective risk of female infidelity and sexual coercion in humans (*Homo sapiens*). *Journal of Comparative Psychology*. 125: 370-373.
- Mosser, A., & Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*. 78: 359-370.

- Nichols, H. J., Amos, W., Cant, M. A., Bell, M. B. V., & Hodge, S. J. 2010. Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose. *Animal Behaviour*. 80: 649-657.
- Nichols, H. J., Cant, M. A., Hoffman, J. I., & Sanderson, J. L. 2014. Evidence for frequent incest in a cooperatively breeding mammal. *Biology Letters*. 10.
- Nichols, H. J., Jordan, N. R., Jamie, G. A., Cant, M. A., & Hoffman, J. I. 2012. Fine-scale spatiotemporal patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry in a cooperatively breeding mammal. *Molecular Ecology*. 21: 5348-5362.
- Nielsen, J. F., English, S., Goodall-Copestake, W. P., Wang, J., Walling, C. A., Bateman, A., Flower, T. P., Sutcliffe, R. L., Samson, J., Thavarajh, N. K., Kruuk, L. E. B., Clutton-Brock, T. H., & Pemberton, J. M. 2012. Inbreeding and inbreeding depression of early life traits in a cooperative mammal. *Molecular Ecology*. 21: 2788-2804.
- Pilot, M., Dahlheim, M. E., & Hoelzel, A. R. 2010. Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *Journal of Evolutionary Biology*. 23: 20-31.
- Reid, J. M., Arcese, P., Keller, L. F., Germain, R. R., Duthie, A. B., Losdat, S., Wolak, M. E., & Nietlisbach, P. 2014. Quantifying inbreeding avoidance through extra-pair reproduction. *Evolution*. 69: 59-74.
- Sambrook, J., Fritsch, E. F., & Maniatis, T. 1989. *Molecular Cloning: A Laboratory Manual*. New York, USA: Cold Spring Harbour Laboratory Press.
- Santos, E. S. A., & Nakagawa, S. 2013. Breeding biology and variable mating system of a population of introduced dunnocks (*Prunella modularis*) in New Zealand. *PLoS ONE*. 8: e69329.
- Sillero-Zubiri, C., & Macdonald, D. W. 1998. Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *Journal of Zoology*. 245: 351-361.
- Suter, S. M., Bielańska, J., Röthlin-Spillmann, S., Strambini, L., & Meyer, D. R. 2009. The cost of infidelity to female reed buntings. *Behavioral Ecology*. 20: 601-608.

Watts, D. P., Muller, M., Amsler, S. J., Mbabzi, G., & Mitani, J. C. 2006. Lethal Intergroup Aggression by Chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*. 68: 161-180.

Wrangham, R., & Glowacki, L. 2012. Intergroup Aggression in Chimpanzees and War in Nomadic Hunter-Gatherers. *Human Nature*. 23: 5-29.

Wrangham, R., Wilson, M., & Muller, M. 2006. Comparative rates of violence in chimpanzees and humans. *Primates*. 47: 14-26.