1 # Reproductive competition triggers mass eviction in cooperative

2 # banded mongooses

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In many vertebrate societies, forced eviction of group members is an important determinant of

population structure, but little is known about what triggers eviction. Three main explanations are

(1) the reproductive competition hypothesis; (2) the coercion of cooperation hypothesis; and (3) the

adaptive forced dispersal hypothesis. The last hypothesis proposes that dominant individuals use

eviction as an adaptive strategy to propagate copies of their alleles through a highly structured

population. We tested these hypotheses as explanations for eviction in cooperatively breeding

banded mongooses (*Mungos mungo*), using a 16-year dataset on life history, behaviour and

relatedness. In this species, groups of females, or mixed-sex groups, are periodically evicted *en

masse*. Our evidence suggests that reproductive competition is the main ultimate trigger for eviction

for both sexes. We find little evidence that mass eviction is used to coerce helping, or as a

mechanism to force dispersal of relatives into the population. Eviction of females changes the

landscape of reproductive competition for remaining males, which may explain why males are

evicted alongside females. Our results show that the consequences of resolving within-group conflict

resonate through groups and populations to affect population structure, with important implications

for social evolution.

Keywords: eviction; conflict; cooperation; reproductive competition; coercion; forced dispersal

Introduction

Individuals living in 'viscous' groups, in which there are severe constraints on dispersal, face

numerous conflicts of interest with other group members. In cooperative breeders, conflict can

arise over reproduction, helping effort, parental care, and dispersal [1–3]. Much theoretical and

empirical work has focused on how individuals resolve these within-group conflicts. In both insect

and vertebrate societies, individuals may use threats, aggression, punishment and various strategies

of negotiation to settle conflicts without breaking up the group [4–6]. In other cases, however,

within-group conflict results in the forcible eviction of one or more group members, typically

following intense, targeted aggression [7–10]. Eviction often leads to the permanent dispersal of

48   individuals, or coalitions of individuals, and may be a major source of gene flow between groups

49   [11,12]. Determining what triggers eviction is therefore important to understand the factors that

50   shape population genetic structure and demography in viscous populations, and hence social

51   evolution [13,14].

52   In social vertebrates, eviction often appears to be driven by conflict over reproductive or social

53   status within groups. In some mammal species, dominant individuals maintain their reproductive

54   monopoly by evicting reproductive competitors from the group [7,15]. For example, in meerkats,

55   *Suricata suricatta*, dominant females evict subordinate females in the latter half of their (own)

56   pregnancy, often as a strategic measure to avoid infanticidal attacks on their pups [16]. Subordinates

57   that are pregnant when evicted experience a deterioration in condition, elevated stress levels, and

58   often spontaneously abort before gaining re-admittance to their group [7]. Consequently, eviction

59   reduces future, as well as current, reproductive competition from the perspective of the dominant

60   by suppressing subordinates' future reproductive success. In fish that form size-based hierarchies,

61   dominant individuals use the threat of eviction to deter subordinates from growing large enough to

62   challenge their position [17–19]. As a result, in the coral dwelling goby, *Paragobiodon xanthosomus*,

63   subordinates starve themselves to avoid triggering eviction [20].

64   Alternative explanations for eviction are based on the idea that dominant individuals can use

65   eviction to coerce their subordinates to help. For example, the pay-to-stay hypothesis [21] suggests

66   that dominant individuals can threaten helpers with eviction unless they behave cooperatively.

67   Additionally, dominant individuals might evict temporarily to coerce helpers to work harder on their

68   return [22], or evict permanently to establish a reputation for punishment and thereby induce

69   remaining helpers to cooperate [23]. Clear evidence in support of such coercive mechanisms comes

70   from the cooperative cichlid, *Neolamprologus pulcher*. Helpers that are experimentally prevented

71   from helping are subject to elevated aggression from dominants and subsequently help more, as

72   predicted if aggression is a signal of impending eviction [9,24]. In addition, helpers that are

73   temporarily removed are often evicted on their return, and those that are reaccepted work harder

74   thereafter [25]. In cooperative birds and mammals evidence for the pay-to-stay hypothesis is less

75   clear-cut. In superb fairy-wrens, *Malurus cyaneus*, temporary removal of helpers results in increased

76   aggression from dominants [26], while in naked mole-rats, *Heterocephalus glaber*, and meerkats

77   there is evidence that uncooperative helpers are subject to aggression from dominant breeders

78   [27,28]. In addition, temporarily evicted female meerkats are more likely to allolactate on their

79   return to the group than non-evicted females [29]. By contrast, studies of bell miners, *Manorina*

80   *melanophrys*, [30,31] and chestnut-crowned babblers, *Pomatostomus ruficep*, [32] have failed to

81   find support for mechanisms based on pay-to-stay or punishment.

82   A third, unexplored hypothesis is that eviction is an adaptive forced dispersal strategy used by

83   breeders to spread copies of their alleles through the wider population. Traditionally, studies of

84   cooperative breeders have used the number of surviving offspring as a measure of fitness. However,

85   groups of cooperative breeders can be thought of as miniature populations embedded within a

86   wider metapopulation [33]. In this kind of structured population, what matters is not just the

87   number of offspring that are successfully raised, but how successful these offspring are at dispersing

88   to form or join new groups, and in turn produce dispersing offspring of their own - sometimes

89   referred to as metapopulation fitness [34,35]. Forced dispersal could be a strategy to maximise

90   metapopulation fitness, over and above any immediate benefits evictors might gain by reducing

91   local competition (although more intense local competition should strengthen selection for forced

92   dispersal). If eviction is primarily a strategy to export copies of alleles, one would expect dominants

93   to evict related individuals rather than unrelated individuals, to evict when local competition is high,

94   and to evict when the evictees have the best chance of dispersing successfully to found or usurp new

95   groups.

96   Banded mongooses, *Mungos mungo*, are a good system to test hypotheses about the causes and

97   function of eviction in cooperative societies because evictions are common and conspicuous. This

98   species lives in mixed-sex groups of around twenty adults, plus offspring. Each eviction event starts

99   suddenly, lasts several days, and involves intense aggression from males and females directed

100   toward multiple individuals. Aggression continues until groups of females, and on occasion groups of

101   males alongside them, are driven away from the group, sometimes limping or bleeding [8] (see the

102   video of a typical eviction event in the Electronic Supplementary Material (ESM)). Up to 26

103   individuals have been observed to be evicted in a single eviction event [8]. Evictees are sometimes

104   allowed to return to their group within a week ('temporary evictions') or they may disperse

105   permanently ('permanent evictions'; [36]). In mixed-sex, permanent eviction events, males and

106   females form same-sex cohorts and disperse separately, most likely to avoid inbreeding [37].

107   In banded mongoose groups there is intense reproductive competition among both males and

108   females [38]. Among males, a few high-ranking 'mate guarding' males aggressively monopolise

109   access to females during oestrus: on average the oldest three males sire 85% of offspring in each

110   group [39]. Most females give birth in each breeding attempt, usually on the same day [40], and the

111   communal litter is reared by the whole group [41,42]. Pups compete for food and access to helpers,

112   and the per capita reproductive success of females declines as the number of breeding females

113   grows large [15]. There is also conspicuous helping behaviour exhibited by both parents and non-

114   parents. Both males and females 'babysit' offspring at the den in the first month after birth [41], and

115   after pups emerge they are guarded and provisioned by adult 'escorts' [43].

116   In this paper we investigated what triggers eviction events in groups of banded mongooses. We

117   tested three distinct but non-exclusive hypotheses: (1) eviction is a response to reproductive

118   competition; (2) eviction is used to coerce cooperation; (3) eviction is an adaptive forced dispersal

119   strategy. We make the following predictions (Table 1). First, if eviction is a response to reproductive

120   competition we predict that an eviction event is more likely to occur when intrasexual competition is

121   high, and when ecological conditions are unfavourable for successful reproduction. Other things

122   being equal, increasing relatedness should reduce the probability of an eviction event, because

123   dominants should be more tolerant of kin competitors [44], and because kinship should reduce

124   competitive effort within groups [45,46]. Second, if eviction is used to coerce helpers we predict a

125   higher probability of eviction following breeding attempts where helping performance was poor,

126 where the outside options for helpers are good [47,48], and where relatedness is low [49]. In

127 addition, if eviction is used as a mechanism to enforce harder work, we expect eviction events to

128 result in improved helping performance in the subsequent breeding attempt. Third, if eviction is a

129 means by which dominants force copies of their alleles into the wider population we expect eviction

130 events to occur when relatedness in the group is high, when local competition is high, and when

131 ecological conditions are favourable for successful dispersal.

132 We tested these predictions using a dataset of 496 breeding attempts for which we had information

133 on group composition, reproductive success, helping behaviour, relatedness, ecological conditions,

134 and whether eviction occurred. Note in this paper we explicitly focus on the factors that trigger

135 group eviction events, rather than on what features of individuals determine the risk of being

136 evicted.

137

138 **Materials and Methods**

139 **(a) Study population and data collection**

140 We studied a population of banded mongooses on the Mweya Peninsula, Queen Elizabeth National

141 Park, Uganda (0°12'S, 27°54'E), between October 1996 and February 2013. Details of habitat are

142 given elsewhere [38]. Daily measurements of temperature and rainfall were recorded by the Uganda

143 Institute of Ecology Meteorological Station and, later, using our own weather station. Over the 16-

144 year study period, we observed 496 breeding attempts in 16 groups. Following [40], we defined a

145 communal litter as one where all pregnant females gave birth within 30 days of one another. We

146 defined a breeding attempt as the 67 day period prior to the birth of each litter (comprised of a 7

147 day oestrus and a 60 day gestation [50]). We defined an eviction event to have occurred in a

148 breeding attempt if one or more individuals left their group for at least one day following a period of

149 intense aggression toward themselves or other group members [15,36]. In practice, evictions are

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150 conspicuous and noisy events that are easy to recognise. Typically, individuals leave only after being

151 repeatedly attacked, but much aggression occurs in the bushes where we are unable to identify the

152 aggressors or their victims. Instances where individuals left their group without any observed

153 aggression toward any group member were defined as voluntary dispersal events and were not

154 considered in our analysis. Groups were visited every 1 to 3 days to record life history and

155 behavioural data. Most were habituated to human presence, allowing observers to watch and follow

156 them from less than 5m. One or two individuals in each group wore a radio collar (Sirtrack Ltd.,

157 Havelock North, New Zealand) with a 20-cm whip antenna (Biotrack Ltd., UK) that enabled groups to

158 be located. Individuals were easily identifiable by either colour-coded plastic collars or, more

159 recently, unique shave markings on their back. Individuals were regularly trapped to maintain these

160 identification markings (see [51] for details). On first capture a 2 mm skin sample was collected from

161 the end of the tail using sterilised scissors for genetic analyses. DNA was extracted and used to

162 assign parentage and estimate relatedness using a panel of 43 polymorphic microsatellite markers

163 (see [52] for further details).

164

165 **(b) Statistical analyses**

166 We used an information-theoretic approach [53] in which we compared the explanatory power of

167 models to investigate the factors that predict the probability that:

168   (i)   an eviction event occurred in a breeding attempt ('Female evictions'). Since females are

169   evicted in every eviction event, we focused the analysis on the factors predicted to influence

170   female eviction;

171   (ii) when an eviction event occurred, males were evicted alongside females ('Male evictions').

172   Here we focused the analysis on the factors predicted to influence male eviction;

173   (iii) when an eviction event occurred, it was temporary rather than permanent ('Temporary

174   evictions'). Since temporary evictions could be either female only or mixed-sex events, we

175   included factors predicted to influence both male and female eviction. An eviction was

176   defined as temporary if more than 50% of the evicted cohort were allowed to return to their

177   group.

178   For each analysis, we constructed a candidate set of models which together provided a

179   comprehensive test of the predictions of our 3 hypotheses: reproductive competition, coercion of

180   cooperation, and adaptive forced dispersal. The models incorporated additive combinations of the

181   main terms predicted to influence eviction probability for the hypotheses, together with specific 2-

182   way interactions where we considered these biologically relevant.

183

184   *(1) Models of eviction as a response to reproductive competition*

185   To test whether an eviction event is more likely to occur when reproductive competition is high, we

186   fitted the number of reproductive competitors at the start of the breeding attempt (denoted B),

187   mean monthly rainfall (mm) (E) in the previous 6 months, the interaction between these social and

188   ecological variables ($B{:}E$), and mean group relatedness (R) as fixed effects. Rainfall and insect

189   abundance are correlated [38,54, Marshall et al., unpublished data] so we expect low rainfall to

190   intensify competition for food resources. In the 'Female evictions' analysis, reproductive competitors

191   were defined as females 10 months and over (10 months is the age at first conception; [15,55]). In

192   the 'Male evictions' analysis, reproductive competitors were defined as males 3 years and over (3

193   years is the first age at which males typically become regular mate guards; [37]). In the 'Temporary

194   evictions' analysis, male and female reproductive competitors were defined as above and fitted as

195   separate fixed effects.

196

197   *(2) Models of eviction as coerced cooperation*

198   The coercion of cooperation hypothesis predicts that eviction should be triggered by poor helper

199   performance, but it is not clear whether animals should respond to the outcome of helping (i.e.

200   reproductive success), or to helping behaviour *per se*. We separately investigated these alternatives

201   by using two indices of helping performance: (i) female reproductive success (C_S); and (ii) helping

202   effort (C_E). We also examined the change in helping performance (ΔC_S or ΔC_E).

203   (i) Female reproductive success, C_S, was defined as the number of emergent pups in the previous

204   breeding attempt, per female that contributed to the communal litter. To account for differences in

205   C_S that could be explained by differences in the amount of help available, we included the number of

206   helpers available to babysit that litter (H) and the interaction between these terms (C_S:H)*. The*

207   interaction term is necessary to capture the difference between the same reproductive outcome

208   achieved with few helpers versus many helpers. We included mean group relatedness (R) and mean

209   monthly rainfall (E) as main effects. In the 'Female evictions' analysis, we defined helpers as females

210   aged 6 months to 3 years, since females younger than 3 years are classed as subordinate and are

211   more likely to participate in helping [43,56]. In the 'Male evictions' analysis, helpers were defined as

212   males aged 6 months to 3 years, since males do not become consistent breeders until around 3

213   years of age and, until then, contribute more to helping [37,57]. In the 'Temporary evictions'

214   analysis, male and female helpers were defined as above and fitted as separate fixed effects.

215   To investigate if eviction is used to coerce helpers to work harder in the subsequent breeding

216   attempt, we tested whether the change in helping performance from one litter to the next predicted

217   the probability that an eviction event occurred in the interim. We reasoned that if eviction is used as

218   a punishment to improve future helping performance, an eviction event (and temporary eviction

219   events in particular) should be associated with an increase in helping performance of remaining or

220   returning helpers after eviction. We fitted ΔC_S, ΔH and the interaction between them (ΔC_S:ΔH) as

221   fixed effects, where ΔC_S is the change in female reproductive success (i.e. the number of emergent

222   pups, per female that contributed to the litter), and ΔH is the change in the number of available

223   helpers, across two consecutive breeding attempts (the breeding attempt before the eviction, and

224   the subsequent breeding attempt). Again, we included mean group relatedness (R) and mean

225   monthly rainfall (E) as fixed effects. Note that ΔC_S and ΔH are likely to be affected by the problem of

226   regression to the mean [58] because extremely high or low values in the first measure of a given

227   variable are more likely to move closer to the mean in a second measure of that variable. We

228   controlled for potential problems with regression to the mean following the methods in [58] (see the

229   ESM).

230   (ii) Helping effort, C_E, was defined as the contribution by helpers (H) to babysitting in the previous

231   breeding attempt (i.e. C_E = number of helpers that babysat per day of babysitting). We repeated the

232   analyses outlined above, replacing C_S with C_E. In the 'Female evictions' analysis, C_E was defined as the

233   number of female babysitters aged 6 months to 3 years left per day of babysitting of the previous

234   litter. In the 'Male evictions' analysis, C_E was defined number of male babysitters aged 6 months to 3

235   years left per day of babysitting of the previous litter. In the 'Temporary evictions' analysis, C_E was

236   defined as in the previous two analyses and fitted as separate fixed effects. In the 'Temporary

237   eviction' analysis, the model including both the change in female helpers' babysitting effort and

238   male helpers' babysitting effort was too complex to fit to the reduced sample of data and so these

239   variables were fitted in separate models. Since data on babysitting behaviour was not available for

240   all breeding attempts, analysis using this helping effort measure of helping performance was

241   performed on a reduced sample (see ESM Table 2, ESM Table 4 and ESM Table 6).

242

243   *(3) Models of eviction as an adaptive forced dispersal strategy*

244   To test whether an eviction event is more likely to occur when relatedness is high, ecological

245   conditions are good and local competition is intense, we fitted mean group relatedness (R), mean

246   monthly rainfall (E), group size (all individuals over 6 months) (G), the interaction between

247   relatedness and rainfall (R:E), and the interaction between relatedness and group size (R:G) as fixed

248   effects. We included group size to allow for the possibility that local resource competition

249   contributes to the timing of eviction events. The interaction between relatedness and rainfall is

250   particularly important to test the prediction that high group relatedness in combination with

251   favourable ecological conditions will make an eviction event more likely to occur. The definitions of

252   R, E and G were consistent across our three analyses. An alternative prediction is that the nature of

253   competition under which adaptive forced dispersal operates could be reproductive, rather than

254   resource related. We fitted an identical set of models to those described above, but replacing G for

255   the number of reproductive competitors (B) in each of the three analyses.

256

257   *Comparing model performance*

258   Models, including a null model containing no fixed effects, were estimated using generalised linear

259   mixed models (GLMM). Group ID was included as a random intercept to control for repeated

260   measures across groups. In all analyses we used the maximum sample size for which we had data on

261   all the terms in all the models (ESM Tables 1-6). In all three analyses, the eviction metric was fitted

262   as the binomial response variable using a logit link function in the lme4 package in R 3.1.2 [59,60].

263   We performed subsets selection of the maximal model under each hypothesis using the 'MuMIn'

264   package [61], which examines all possible combinations of terms in each full model. Models were

265   ranked by Akaike's Information Criteria (AIC), or corrected AIC (AICc) in analyses where $N/k < 40$,

266   where N is the sample size and k is the number of parameters in the maximal model [53]. We

267   defined a 'top model set' as models $\leq \Delta 6$ AIC (or AICc) units of the best supported model [62], after

268   excluding any models where a simpler nested version attained stronger support (applying the

269   'nesting rule' of [62]). Full model tables are provided in the ESM.

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11

271   **Results**

272   *Observations of eviction*

273   In total, we observed 47 eviction events in 8 out of 16 groups in our population between October

274   1996 and February 2013 resulting in the expulsion of 457 individuals. More females than males were

275   evicted; in the 46 events for which we knew the sex and identities of the evictees, evictions resulted

276   in the expulsion of 274 females and 170 males, with the median evicted cohort comprising 24% of

277   the total group (range 3% - 60%). Just 3 eviction events (6%) resulted in the eviction of a single

278   individual. In 25 (53%) of eviction events only females were evicted, with a median of 6 females

279   evicted in a single event (range 1-12). On average, an eviction event resulted in the expulsion of 40%

280   of female group members (range 6% - 79%). In the remaining 22 eviction events (47%) a cohort of

281   males was evicted alongside a cohort of females. In these cases the median number of evictees was

282   13 individuals (range 6-26); median number of female evictees was 6 (range 2-15) and median

283   number of male evictees was 9 (range 1-17). On average, an eviction event resulted in the expulsion

284   of 35% of male group members (range 3% - 65%). Males were only ever evicted alongside females.

285   In 8 out of 22 mixed-sex evictions (36%), some or all of both sexes dispersed permanently as a

286   consequence of eviction. In all these cases, the evicted cohorts of males and females split into single-

287   sex groups and dispersed separately. In 47% of all eviction events, all evictees were eventually

288   readmitted to their group after persistently attempting to re-join. In 32%, some evicted individuals

289   (both males and females) were allowed to return but others were not. Of temporarily evicted

290   individuals, 69% were readmitted to their group within 1 week, 97% within 1 month, and all

291   individuals within 6 months of eviction.

292

Testing the hypotheses

(i) Female evictions

Models of the reproductive competition hypothesis were by far the best predictors of the probability

of an eviction event occurring during a breeding attempt (Table 2). Specifically it was the model

containing the number of breeding females that performed the best out of the candidate model set,

with an eviction event more likely to occur when there were more breeding females (Figure 1).

Models of the reproductive competition hypothesis had a cumulative adjusted Akaike's model

weight of 100% of retained models from the top model set when helping performance was

measured in terms of female reproductive success (C_S) (Table 2), and 95% when helping

performance was measured in terms of helping effort (C_E) (ESM Table 2).

(ii) Male evictions

The probability that males were evicted with females, given that an eviction occurred, was also best

explained by the reproductive competition hypothesis (analysis using the female reproductive

success (C_S) measure of helping performance). Specifically, the model that performed best contained

the number of breeding males (Table 3), with males more likely to be evicted with females as the

number of breeding males increased (Figure 2). The only other model to be retained after applying

the nesting rule [62] was the model of adaptive forced dispersal containing group size and mean

group relatedness, with males more likely to be evicted alongside females in larger groups and when

group relatedness was low, although this model only attained an adjusted weight of 5%. When

performing the same analysis but using the helping effort (C_E) measure of helping performance on a

reduced sample size, the only model that was retained was the null model which contained an

intercept but no fixed effects (ESM Table 4).

315   *(iii) Temporary evictions*

316   None of our hypotheses explained whether eviction events were temporary rather than permanent.

317   The null model performed better than all other models and this result was consistent whether

318   female reproductive success (C_S) or helping effort (C_E) was used as a measure of helping

319   performance (ESM Table 5 and ESM Table 6).

320

321   **Discussion**

322   Previous work on eviction in this species highlighted reproductive competition as a driver of female

323   evictions, but did not consider male or temporary evictions, or test alternative hypotheses for

324   eviction behaviour [8,15,36]. For both female and mixed-sex eviction events, the reproductive

325   competition hypothesis best explained our data. Females were more likely to be evicted when there

326   were many breeding females in the group. These female eviction events are likely to radically alter

327   the landscape of intrasexual competition among remaining males, which may explain why groups of

328   males are commonly evicted alongside females. Males were more likely to be evicted when there

329   were many breeding males in the group, again supporting the hypothesis that high levels of same-

330   sex reproductive competition is a trigger for mass eviction.

331   Sex differences in the intensity of reproductive competition may explain why evictions of females

332   are almost twice as common as male evictions. Reproductive competition is particularly intense

333   among female banded mongooses because dominants are unable to suppress reproduction by

334   younger females and suffer substantial fitness costs when large numbers of subordinate females

335   breed alongside them [15,56]. Dominant males, by contrast, can usually prevent subordinate males

336   from mating, and so are less sensitive to the presence of additional males in the group. However,

337   dominant males are not immune from reproductive competition because they cannot fully control

338   the mating behaviour of females [39,50]. Dominant males might also evict (usually younger)

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339   subordinates before these become genuine reproductive competitors, similar to the explanations for

340   eviction in size-based fish hierarchies [17–20]. At the same time, young male banded mongooses

341   that are excluded from breeding have less to gain from putting up a fight to stay in their natal group

342   compared to females. This potential difference in the level of resistance offered could explain why

343   males sometimes disperse voluntarily, while female dispersal events almost always involve intense

344   aggression.

345   We found little evidence to support the idea that mass evictions are triggered when it is adaptive for

346   dominants to force subordinates to disperse. We did find weak support for a model that showed

347   that males were more likely to be evicted with females when groups were large, but when mean

348   group relatedness was low. This effect of relatedness is the opposite of that predicted under the

349   adaptive forced dispersal hypothesis. Eviction of either sex was not more likely when mean group

350   relatedness was high, nor when ecological conditions were benign. We cannot rule out adaptive

351   forced dispersal entirely, however, because (1) we currently lack information about the long term

352   fate of evictees in the wider population; and (2) we currently lack a formal model of the adaptive

353   forced dispersal hypothesis which might provide discriminating predictions beyond those based on

354   our simple verbal arguments. Concerning point (1), eviction did result in the permanent dispersal of

355   193 individuals, which is 72% of the individuals in our population that left their natal group [37].

356   Eviction is therefore likely to be a major determinant of gene flow and population structure in this

357   system. Concerning (2), demographic models of kin selection [13,63] usually assume that dispersal is

358   under the full control of the offspring themselves, or under full maternal control (e.g. [64], but see

359   [65]). Our observations of eviction, by contrast, suggest that in many real systems, no single party

360   has full control over group membership, and group dynamics are a compromise between the

361   interests of evictors and evictees. A model embedding a conflict resolution mechanism (e.g. similar

362   to Higashi and Yamamura's [44] insider-outsider conflict model) in a demographic framework could

363   be a useful tool to predict population consequences of reproductive competition.

364   Finally, we found little evidence to support the coercion of cooperation hypothesis for mass eviction

365   in this system. This contrasts with strong evidence that eviction, and the threat of eviction, is used to

366   coerce helpers to work harder in the cooperative cichlid *N. pulcher* [9,24,25,49,66]. Why should

367   eviction be effective to coerce cooperation in cichlids but not banded mongooses? We suggest two

368   reasons. First, theory suggests that acts and threats of eviction will be much less effective at coercing

369   cooperation when targeted at a group of individuals rather than specific individual helpers [15]. In a

370   group of helpers, the threat of mass eviction creates a tragedy-of-the-commons over helping effort

371   since the effort of any hard working helper can be readily exploited by the idleness of other

372   potential evictees. Eviction is likely to be much more effective at inducing cooperation when

373   targeted at individual transgressors, for example in dyads and in groups which exhibit a strict rank

374   hierarchy (such as cooperative cichlids; [9,19,49]). Second, threats of eviction are predicted to be

375   less effective at inducing pre-emptive cooperation when evictees are often reaccepted into the

376   group, as in banded mongooses ([15]; this paper) and meerkats [16]. The best tests of the coercion

377   of cooperation hypothesis require experimental reduction of helper effort [9,24], or manipulation of

378   the availability of outside options [66,67], which is logistically challenging in birds and mammals.

379   Further innovative experimental tests in a wider range of cooperative vertebrates would help to test

380   the coercion of cooperation hypothesis more rigorously.
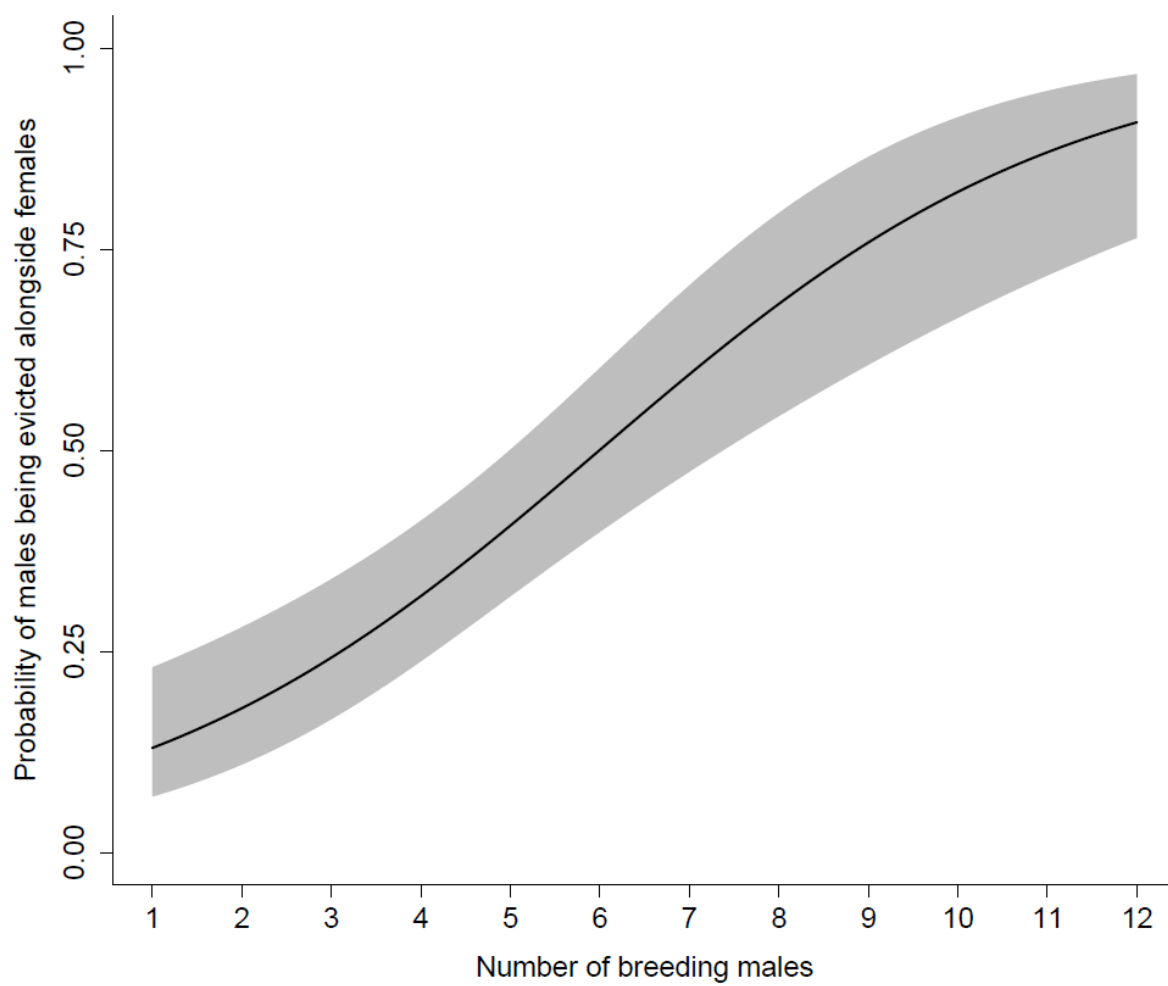
381   To summarise, our results suggest that intrasexual reproductive competition is the trigger for mass

382   eviction of both sexes from groups of banded mongooses. Eviction of females appears to alter the

383   landscape of intrasexual competition among males, leading to the mass eviction of males at the

384   same time as, but separate from, the eviction of females. We did not find evidence to link eviction

385   events to the enforcement of helping or the propagation of alleles through a structured population.

386   Nevertheless, our study highlights that the consequences of resolving within-group reproductive

387   competition can scale up to affect population structure and demography. This link between within-

388   group conflict strategies and population processes has been little studied theoretically or

389   empirically, but may be an important determinant of life history evolution in viscous animal

390   societies.
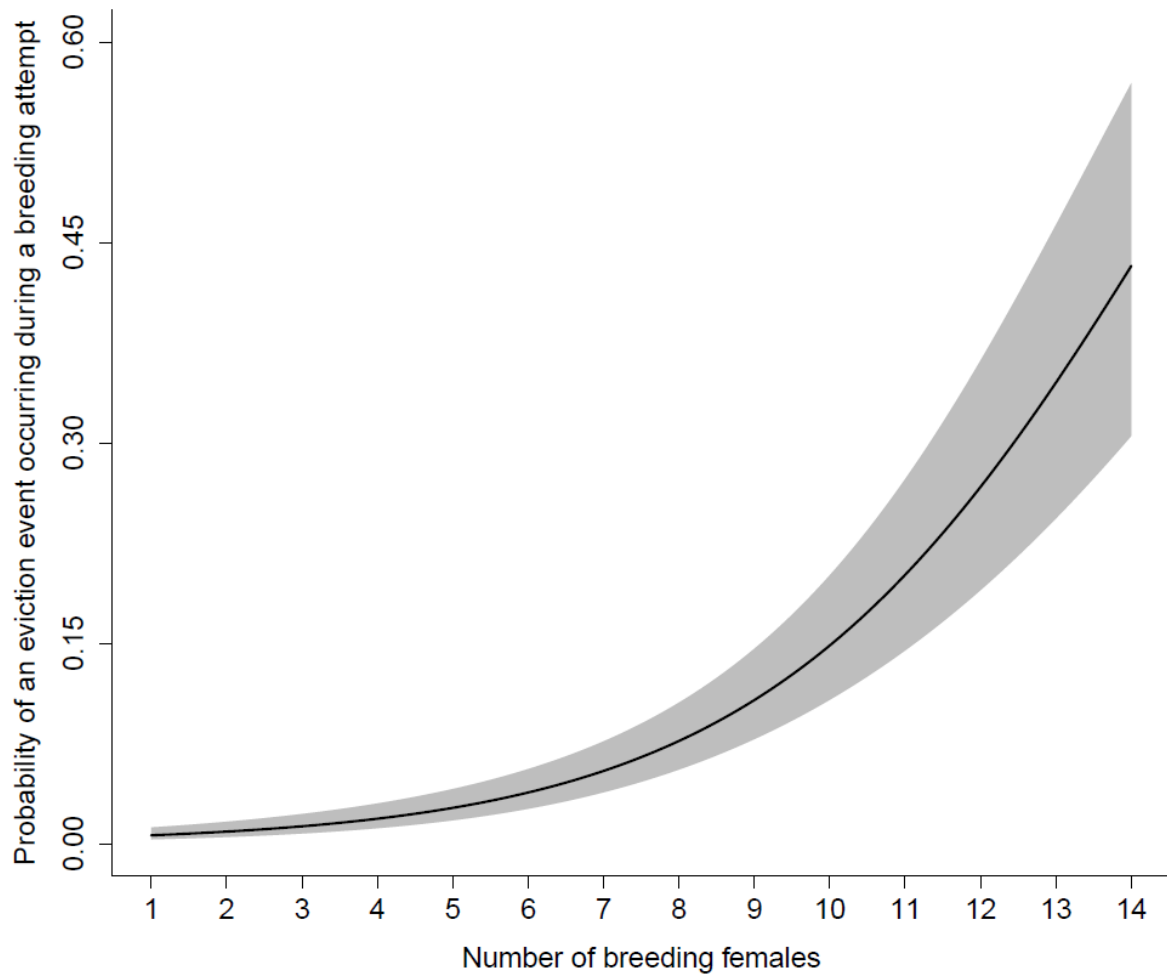
391
392   Figure 1

393
394   Figure 2

Author Contributions

FT, MC, SH and AY conceived the study. FT and MC designed the analyses. FT, HM, JS, EV, JG and SH

collected data. FT analysed data. JS and HN carried out genetic analyses. FT and MC drafted the

paper. All authors contributed to the final version of the manuscript.

415

416   **Data Accessibility**

417   Data is available from the Dryad Digital Repository: doi:10.5061/dryad.8c26b

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586

587 Table 1: Predicted effects of social and environmental variables on the probability of eviction under

588 the three hypotheses described in the text. Numbered references provide theoretical or empirical

589 support for the predictions.

Hypothesis	Number of Competitors	Quality of ecological conditions	Prior helping performance*	Change in helping performance* following eviction	Mean group relatedness
Reproductive Competition	More same-sex competitors → more intrasexual competition → more evictions	Poorer conditions → more intrasexual competition → more evictions	No clear prediction	No clear prediction	Lower relatedness → more intrasexual competition [45,46] → more evictions
Coercion of Cooperation	No clear prediction	Better conditions → groups less stable [48], or helpers work less hard [47] → more evictions	Poorer helping performance → more evictions	Positive change → more evictions	Lower relatedness → groups less stable [48], or more coercion required [49] → more evictions
Adaptive Forced Dispersal	Larger group size → more resource competition → more evictions Or More same-sex competitors → more reproductive competition → more evictions	Better conditions → more successful dispersal → more evictions	No clear prediction	No clear prediction	Higher relatedness → forced dispersal more effective → more evictions

590 * measured by outcome or helping effort

25

Hyp.	Int.	B	E	R	B:E	R:B	R:E	k	logLik	AIC	ΔAIC	w_i	Retained	Adj. w_i
R	-5.44	0.37						3	-108.63	223.26	0.00	0.34	✓	1.00
A	-3.34	0.11		-14.46		1.76		5	-107.25	224.50	1.24	0.18		
A/R	-5.49	0.37		0.42				4	-108.62	225.25	1.99	0.13		
R	-5.45	0.37	0.00					4	-108.63	225.26	2.00	0.13		
A	-3.29	0.11	0.00	-14.52		1.77		6	-107.25	226.50	3.24	0.07		
A/R	-5.51	0.37	0.00	0.43				5	-108.62	227.24	3.99	0.05		
R	-5.37	0.36	0.00		0.00			5	-108.63	227.26	4.00	0.05		
A	-3.34	0.11	0.00	-14.11		1.77	-0.01	7	-107.25	228.49	5.23	0.02		
A	-5.25	0.37	0.00	-1.44			0.03	6	-108.60	229.21	5.95	0.02		
R	-5.42	0.36	0.00	0.44	0.00			6	-108.62	229.24	5.98	0.02		

595 Hyp. = Hypothesis: A = Adaptive Forced Dispersal; R = Reproductive Competition. Columns 2 to 7 show parameter effect

596 sizes from GLMMs on the logit scale: Int. = Intercept; B = number of breeding females; E = mean rainfall in previous 6

597 months; R = mean group relatedness; : = interaction. k = number of estimated parameters including a random intercept

598 for group ID; logLik = log-likelihood; AIC = Akaike's information criterion; ΔAIC = change in AIC value from the best

599 performing model; w_i = Akaike's model weight; Retained = ticks indicate that the model was retained after applying the

600 nesting rule of [62]; Adj. w_i = adjusted Akaike's model weight for the retained models. Blank cells indicate that the term

601 was absent from that model.

602 Table 3: 'Male evictions'. Model performance in predicting the probability that males are evicted

603 alongside females when an eviction event occurs (*N*=37 eviction events in 7 groups). Analysis using

604 the female reproductive success (C_S) measure of helping performance under the coercion of

605 cooperation hypothesis. Models comprise the top model set where ΔAICc ≤ 6.

Hyp.	Int.	*B*	*E*	*R*	*B:E*	*R:B*	*G*	k	logLik	AICc	ΔAICc	*wᵢ*	Retained	Adj. *wᵢ*
R	-2.28	0.38						3	-20.42	47.57	0.00	0.51	✓	0.95
R	-1.81	0.39	-0.01					4	-20.32	49.88	2.32	0.16		
A/R	-2.16	0.38		-0.68				4	-20.41	50.07	2.51	0.15		
R	-0.30	-0.10	-0.04		0.01			5	-19.78	51.51	3.94	0.07		
A	-0.94	0.11		-9.71		2.02		5	-20.24	52.41	4.85	0.05		
A/R	-1.64	0.39	-0.01	-0.90				5	-20.31	52.55	4.98	0.04		
A	-3.82			-1.58			0.15	4	-22.08	53.41	5.84	0.03	✓	0.05

606 Hyp. = Hypothesis: A = Adaptive Forced Dispersal; R = Reproductive Competition. Column headings as in Table 2, with the

607 addition of *G* = group size; AICc = corrected Akaike's information criterion; ΔAICc = change in AICc value from the best

608 performing model. Ticks indicate that the model was retained after applying the nesting rule of [62]. Blank cells indicate

609 that the term was absent from that model.

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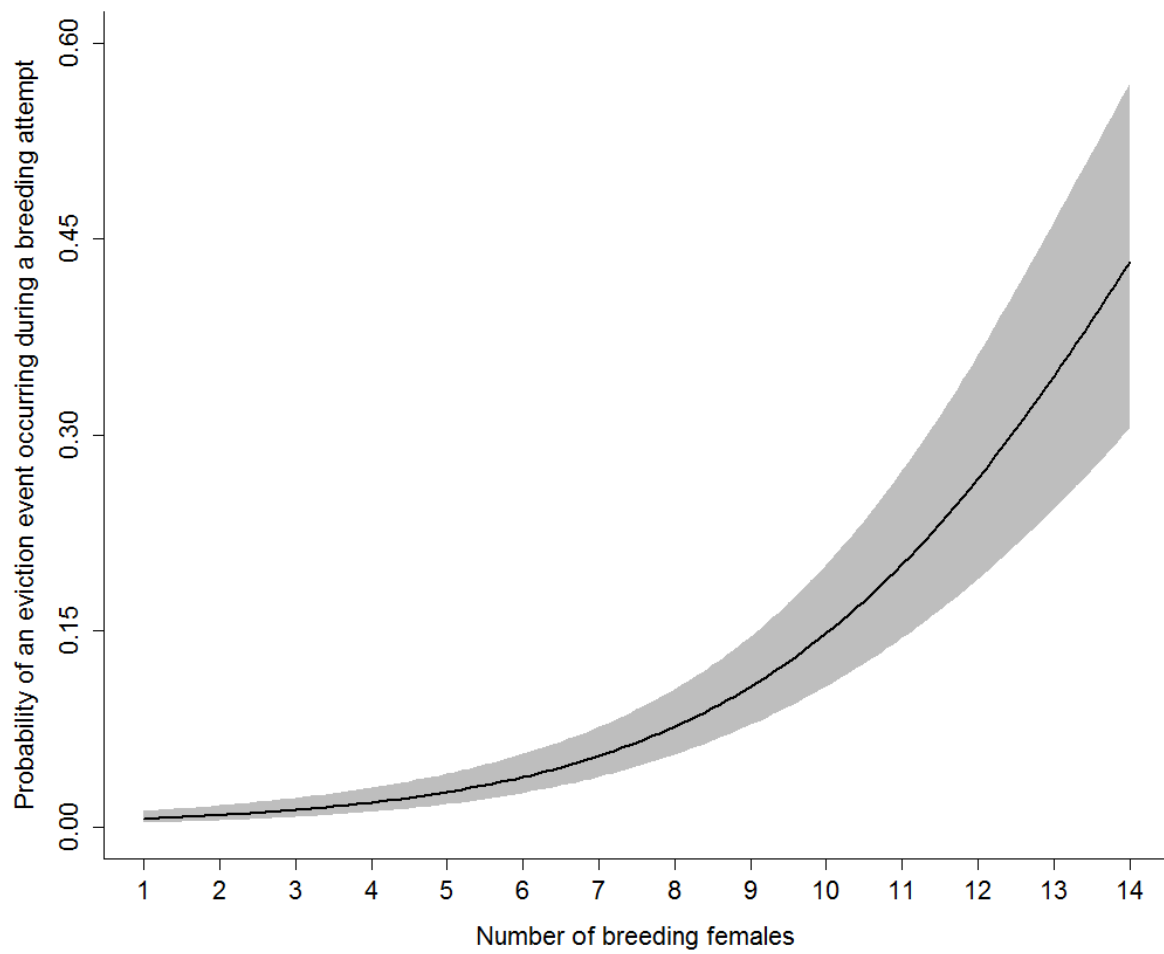
Figure 1: The probability of an eviction event occurring during a breeding attempt against the

number of breeding females (N=415 breeding attempts in 15 groups). The line shows model

predictions (± standard error).

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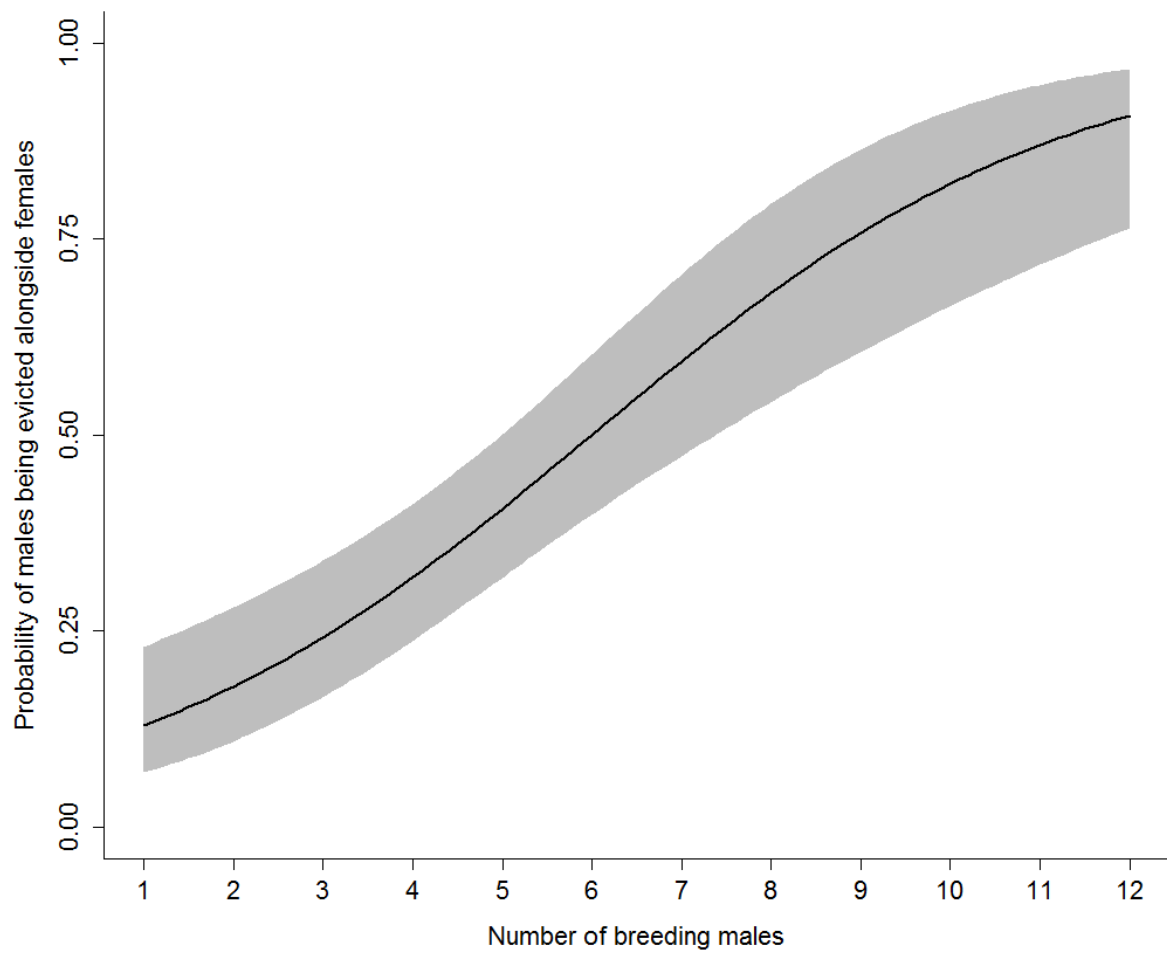
Figure 2: The probability that males are evicted alongside females when an eviction event occurs

(*N*=37 eviction events in 7 groups). The line shows model predictions (± standard error).