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1 Reproductive competition triggers mass eviction in cooperative
2 banded mongooses

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22 In many vertebrate societies, forced eviction of group members is an important determinant of
23 population structure, but little is known about what triggers eviction. Three main explanations are
24 (1) the reproductive competition hypothesis; (2) the coercion of cooperation hypothesis; and (3) the
25 adaptive forced dispersal hypothesis. The last hypothesis proposes that dominant individuals use
26 eviction as an adaptive strategy to propagate copies of their alleles through a highly structured
27 population. We tested these hypotheses as explanations for eviction in cooperatively breeding
28 banded mongooses (*Mungos mungo*), using a 16-year dataset on life history, behaviour and
29 relatedness. In this species, groups of females, or mixed-sex groups, are periodically evicted *en*
30 *masse*. Our evidence suggests that reproductive competition is the main ultimate trigger for eviction
31 for both sexes. We find little evidence that mass eviction is used to coerce helping, or as a
32 mechanism to force dispersal of relatives into the population. Eviction of females changes the
33 landscape of reproductive competition for remaining males, which may explain why males are
34 evicted alongside females. Our results show that the consequences of resolving within-group conflict
35 resonate through groups and populations to affect population structure, with important implications
36 for social evolution.

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

38

39 **Introduction**

40 Individuals living in ‘viscous’ groups, in which there are severe constraints on dispersal, face
41 numerous conflicts of interest with other group members. In cooperative breeders, conflict can
42 arise over reproduction, helping effort, parental care, and dispersal [1–3]. Much theoretical and
43 empirical work has focused on how individuals resolve these within-group conflicts. In both insect
44 and vertebrate societies, individuals may use threats, aggression, punishment and various strategies
45 of negotiation to settle conflicts without breaking up the group [4–6]. In other cases, however,
46 within-group conflict results in the forcible eviction of one or more group members, typically
47 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 babbblers, *Pomatostomus ruficeps*, [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

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 ($\Delta C_S:\Delta H$) 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.

270

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

293 *Testing the hypotheses*

294 *(i) Female evictions*

295 Models of the reproductive competition hypothesis were by far the best predictors of the probability
296 of an eviction event occurring during a breeding attempt (Table 2). Specifically it was the model
297 containing the number of breeding females that performed the best out of the candidate model set,
298 with an eviction event more likely to occur when there were more breeding females (Figure 1).

299 Models of the reproductive competition hypothesis had a cumulative adjusted Akaike's model
300 weight of 100% of retained models from the top model set when helping performance was
301 measured in terms of female reproductive success (C_S) (Table 2), and 95% when helping
302 performance was measured in terms of helping effort (C_E) (ESM Table 2).

303 *(ii) Male evictions*

304 The probability that males were evicted with females, given that an eviction occurred, was also best
305 explained by the reproductive competition hypothesis (analysis using the female reproductive
306 success (C_S) measure of helping performance). Specifically, the model that performed best contained
307 the number of breeding males (Table 3), with males more likely to be evicted with females as the
308 number of breeding males increased (Figure 2). The only other model to be retained after applying
309 the nesting rule [62] was the model of adaptive forced dispersal containing group size and mean
310 group relatedness, with males more likely to be evicted alongside females in larger groups and when
311 group relatedness was low, although this model only attained an adjusted weight of 5%. When
312 performing the same analysis but using the helping effort (C_E) measure of helping performance on a
313 reduced sample size, the only model that was retained was the null model which contained an
314 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)

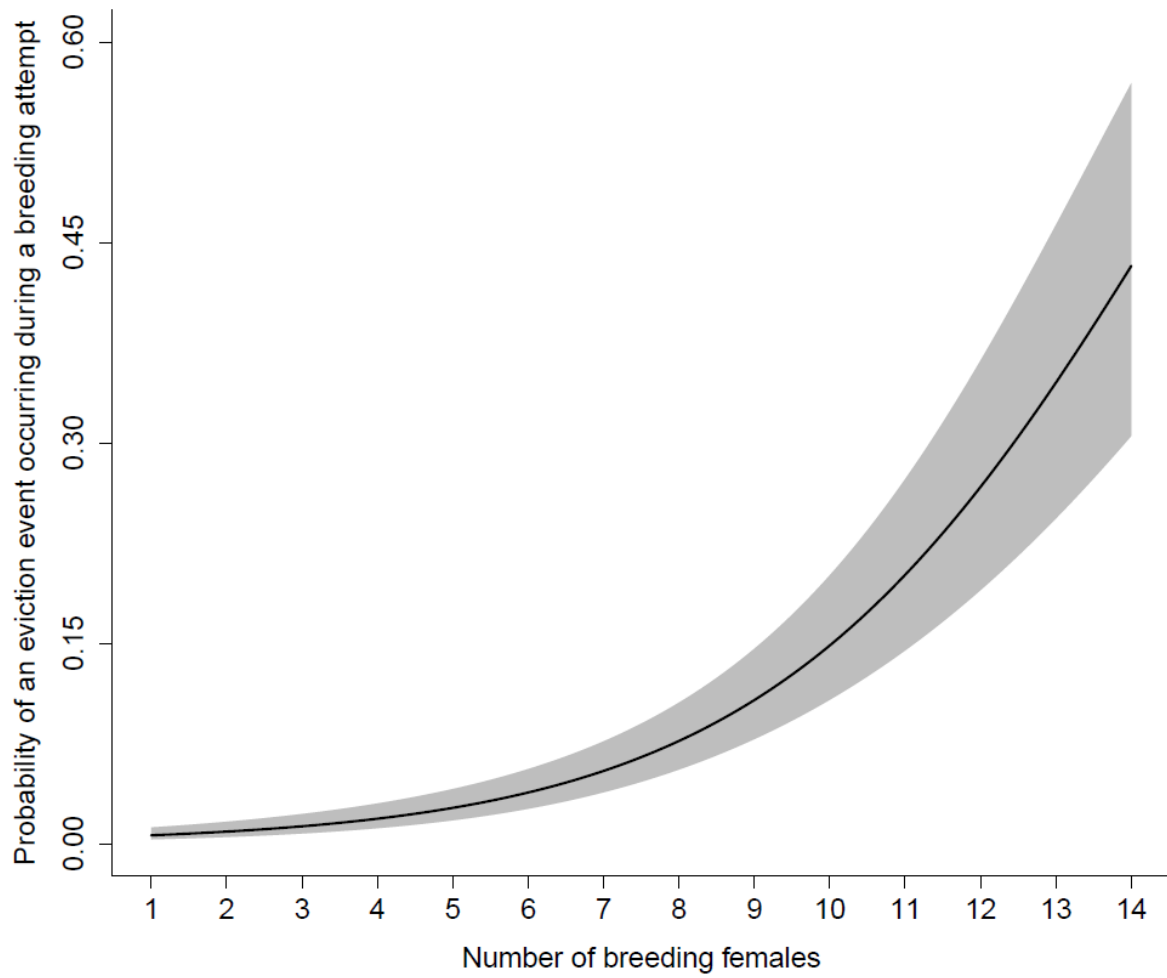
339 subordinates before these become genuine reproductive competitors, similar to the explanations for
340 eviction in size-based fish hierarchies [17–20]. At the same time, young male banded mongooses
341 that are excluded from breeding have less to gain from putting up a fight to stay in their natal 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.

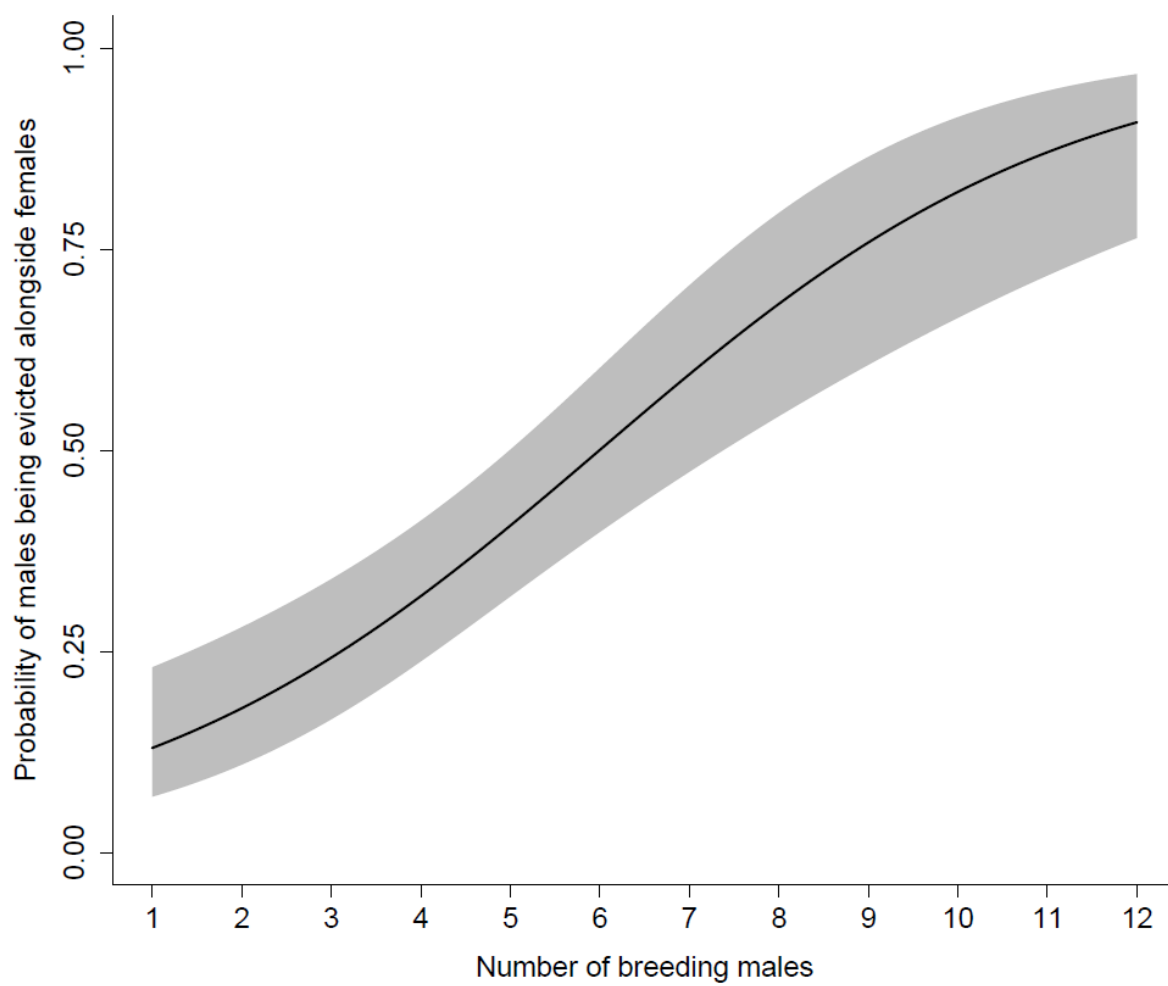
364 Finally, we found little evidence to support the coercion of cooperation hypothesis for mass eviction
365 in this system. This contrasts with strong evidence that eviction, and the threat of eviction, is used to
366 coerce helpers to work harder in the cooperative cichlid *N. pulcher* [9,24,25,49,66]. 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

395

396 **Ethical Statement**

397 All research procedures received prior approval from Uganda Wildlife Authority and Uganda
398 National Council for Science and Technology, and adhered to the Guidelines for the Treatment of
399 Animals in Behavioural Research and Teaching, published by the Association for the Study of Animal
400 Behaviour. All research was approved by the Ethical Review Committee of the University of Exeter.

401

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410

411 **Author Contributions**

412 FT, MC, SH and AY conceived the study. FT and MC designed the analyses. FT, HM, JS, EV, JG and SH
413 collected data. FT analysed data. JS and HN carried out genetic analyses. FT and MC drafted the
414 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](https://doi.org/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

591 Table 2: ‘Female evictions’. Model performance in predicting the probability of an eviction event
 592 occurring during a breeding attempt ($N=415$ breeding attempts in 15 groups). Analysis using the
 593 female reproductive success (C_5) measure of helping performance under the coercion of cooperation
 594 hypothesis. Models comprise the top model set where $\Delta AIC \leq 6$.

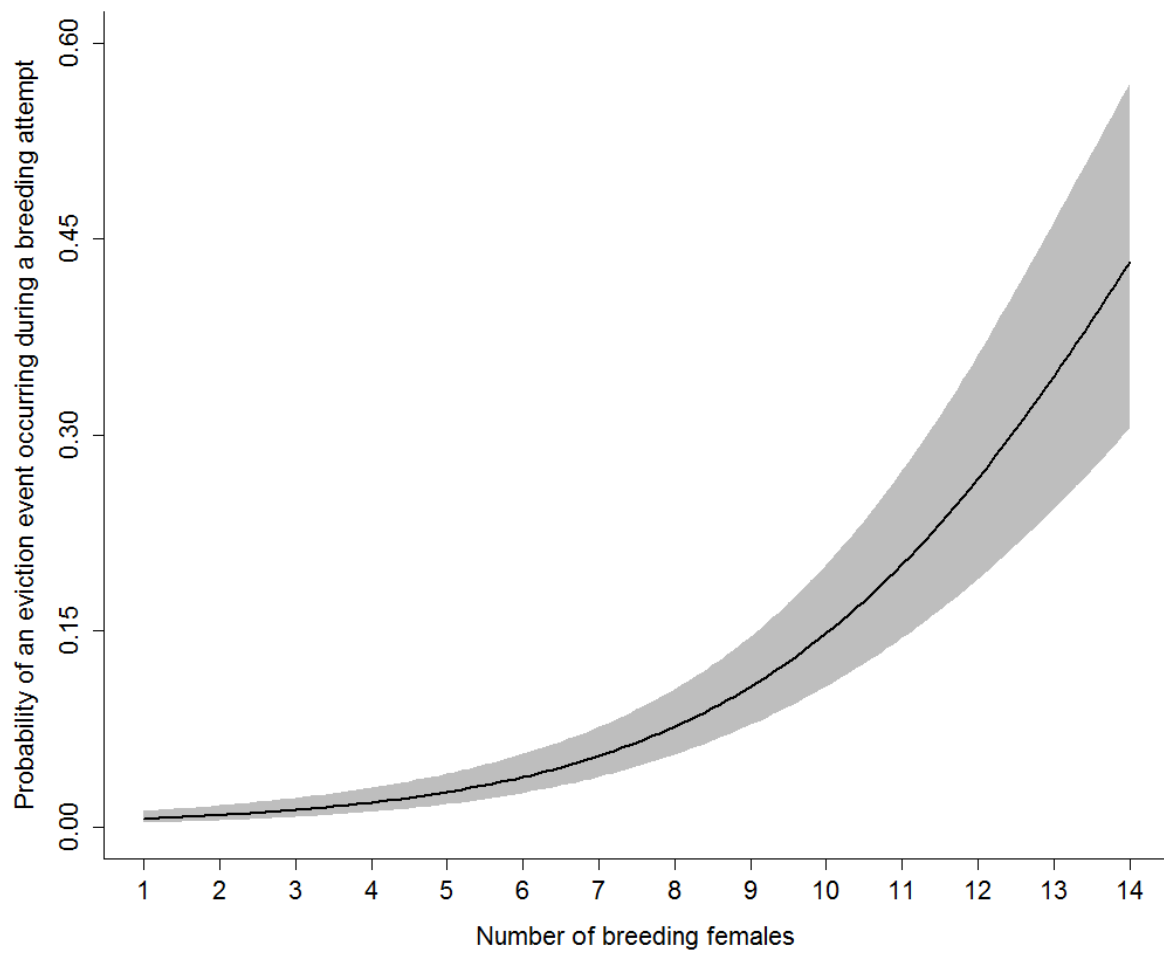
Hyp.	Int.	B	E	R	B:E	R:B	R:E	k	logLik	AIC	ΔAIC	w_i	Retained	Adj. w_i
R	-5.44	0.37						3	-108.63	223.26	0.00	0.34	✓	1.00
A	-3.34	0.11		-14.46		1.76		5	-107.25	224.50	1.24	0.18		
A/R	-5.49	0.37		0.42				4	-108.62	225.25	1.99	0.13		
R	-5.45	0.37	0.00					4	-108.63	225.26	2.00	0.13		
A	-3.29	0.11	0.00	-14.52		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 $\Delta AICc \leq 6$.

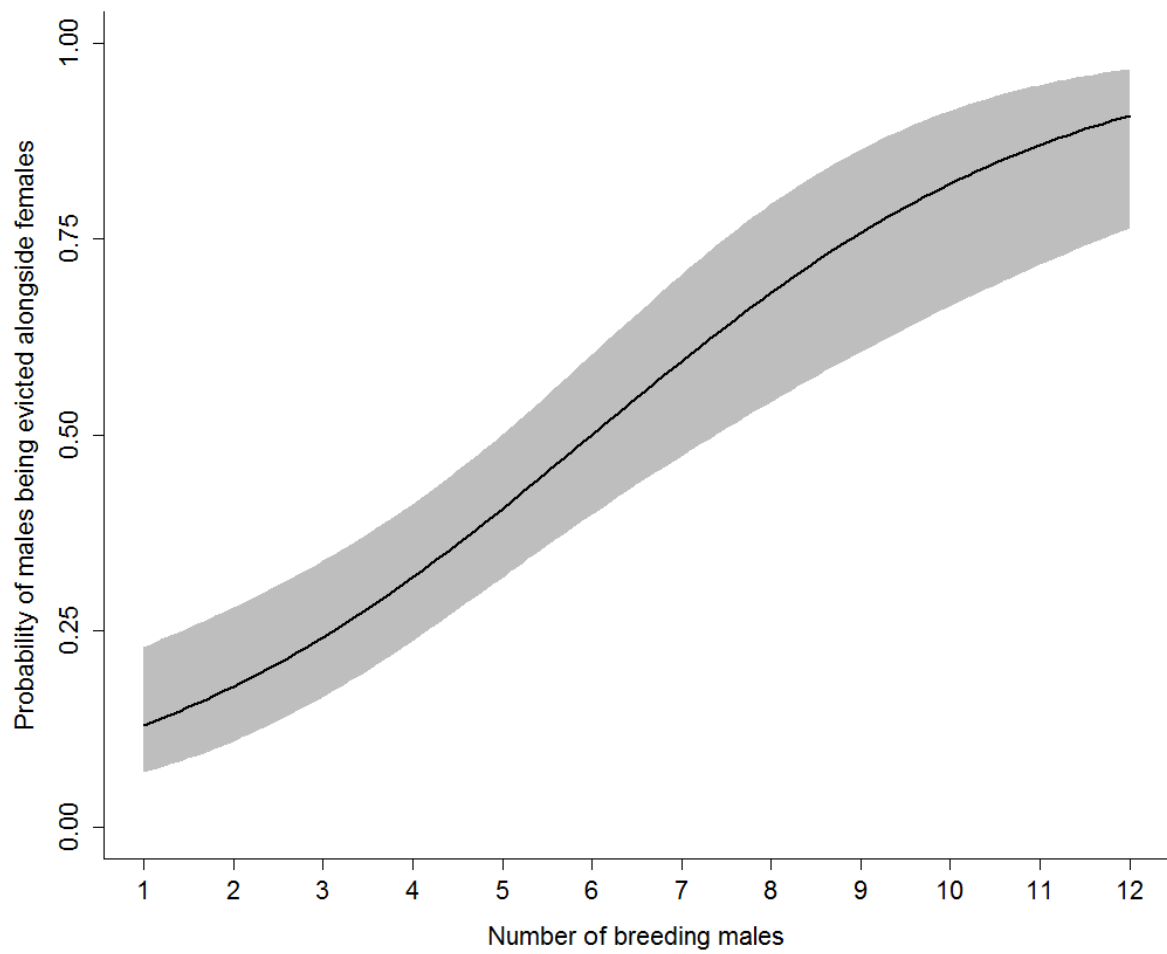
Hyp.	Int.	B	E	R	B:E	R:B	G	k	logLik	AICc	$\Delta AICc$	w_i	Retained	Adj. w_i
R	-2.28	0.38						3	-20.42	47.57	0.00	0.51	✓	0.95
R	-1.81	0.39	-0.01					4	-20.32	49.88	2.32	0.16		
A/R	-2.16	0.38		-0.68				4	-20.41	50.07	2.51	0.15		
R	-0.30	-0.10	-0.04		0.01			5	-19.78	51.51	3.94	0.07		
A	-0.94	0.11		-9.71		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; $\Delta AICc$ = 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.



610

611 Figure 1: The probability of an eviction event occurring during a breeding attempt against the
612 number of breeding females ($N=415$ breeding attempts in 15 groups). The line shows model
613 predictions (\pm standard error).



614

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

616 ($N=37$ eviction events in 7 groups). The line shows model predictions (\pm standard error).