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**BIOLOGY
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Manuscripts

1 **Evidence for frequent incest in a cooperatively breeding mammal**

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7 **Short title:** Inbreeding in a cooperative breeder

8

9 **Summary**

10 As breeding between relatives often results in inbreeding depression, inbreeding avoidance is
11 widespread in the animal kingdom. However, inbreeding avoidance may entail fitness costs. For
12 example, dispersal away from relatives may reduce survival. How these conflicting selection
13 pressures are resolved is challenging to investigate, but theoretical models predict that inbreeding
14 should occur frequently in some systems. Despite this, few studies have found evidence of regular
15 incest in mammals, even in social species where relatives are spatiotemporally clustered and
16 opportunities for inbreeding frequently arise. We used genetic parentage assignments together with
17 relatedness data to quantify inbreeding rates in a wild population of banded mongooses, a
18 cooperatively breeding carnivore. We show that females regularly conceive to close relatives,
19 including fathers and brothers. We suggest that the costs of inbreeding avoidance may sometimes
20 outweigh the benefits, even in cooperatively breeding species where strong within-group incest
21 avoidance is considered to be the norm.

22

23 **Introduction**

24 Breeding between close relatives has long been recognised to entail a fitness cost, known as
25 inbreeding depression, which is thought to result mainly from the unmasking of harmful recessive
26 alleles [1]. Consequently, it is not surprising that inbreeding avoidance mechanisms such as dispersal,
27 reproductive restraint and mating with unfamiliar individuals are widespread in the animal kingdom
28 [1]. However, inbreeding avoidance can also entail fitness costs. For example, dispersal is commonly
29 associated with increased mortality [2]. By implication, even inbreeding between first-order relatives
30 should be tolerated under some circumstances [3, 4].

31 Although inbreeding and inbreeding avoidance have fitness consequences in virtually all
32 vertebrates, these effects may be particularly important in cooperative breeders, where natal
33 philopatry can lead to the presence of sexually mature relatives in social groups [5]. Moreover,
34 theoretical work predicts that inbreeding could have a substantial positive effect on inclusive fitness
35 in these species by increasing the reproductive success of relatives [6] and/or increasing the benefits
36 of cooperation [5, 7].

37 Despite these theoretical predictions, evidence that incest forms a regular part of the mating
38 system of mammalian cooperative breeders is scarce and the vast majority of these species appear
39 to have obvious within-group inbreeding avoidance mechanisms [5]. Furthermore, in the handful of
40 species where frequent incest is thought to occur, such as naked mole rats, genetic data are either
41 lacking or insufficient to quantify inbreeding [2, 4, 5].

42 Here, we use an unusually large genetic dataset in combination with detailed behavioural
43 observations to investigate inbreeding in the banded mongoose (*Mungos mungo*), a cooperatively
44 breeding carnivore that lives in mixed-sex groups (median group size = 18 adults). Groups consist of
45 a ‘core’ of dominant individuals (1–5 females and 3–7 males) that reproduce 3–4 times per year,
46 alongside younger subordinates that breed occasionally. Although some dispersal occurs, many

47 individuals of both sexes remain in the natal group for their entire lives [8]. Both sexes also
48 frequently breed in their natal group, despite the presence of first order relatives, and there is no
49 evidence of reproductive restraint [9]. Immigration of individuals into established groups is
50 practically absent [8] so opportunities to mate with unrelated immigrants rarely arise. Furthermore,
51 pups are reared in large communal litters, making familiarity an ineffective cue to relatedness [8]. In
52 the absence of any obvious mechanism of within-group inbreeding avoidance, a previous study
53 suggested that inbreeding could be a regular part of the banded mongoose mating system [9].

54 New banded mongoose groups form when a cohort of female relatives from one natal group
55 joins a cohort of male relatives from a different natal group, resulting in opposite sex group-
56 members initially being unrelated [8]. However, due to high levels of philopatry and a lack of
57 immigration, relatedness between opposite-sex breeders builds up over time [10], suggesting that
58 inbreeding could be more prevalent in older groups. Inbreeding might also be more likely to occur
59 when groups are small and choice over mating partners is restricted. Nevertheless, it is also possible
60 that females avoid inbreeding by mating with extra-group males. Although observations of extra-
61 group copulations are rare, neighbouring territories often overlap substantially and groups
62 encounter each other regularly, so opportunities may arise [10].

63 We use 20 microsatellite markers to assign parentage and to generate a partial pedigree for
64 an intensively studied population of banded mongooses. We quantify the frequency with which
65 females breed within their natal group and test the hypothesis that females mate with close
66 relatives. We also test the predictions that inbreeding is prevalent in older and smaller social groups,
67 and that females can avoid inbreeding through dispersal or mating with extra-group males.

68

69 **Methods**

70 *Behavioural data*

71 We studied a population of 14 banded mongoose groups living in Queen Elizabeth National
72 Park, Uganda ($0^{\circ}12'S$; $29^{\circ}53'E$) between November 1995 and September 2011. All animals were
73 marked individually and habituated to close observation (< 5 m). Groups were observed every 1-4
74 days, allowing individuals to be tracked from birth to death and all dispersal and breeding events to
75 be recorded [8]. Average adult survival in our Ugandan population (females 0.61, males 0.66) is
76 similar to that found in the Serengeti (females 0.69, males 0.65) so it is unlikely that any observed
77 inbreeding is due to unusually high survival in our study population [11].

78 *Parentage analysis*

79 A total of 1534 tail tip samples were collected using sterile scissors while animals were
80 anesthetised. Further details of sample collection and genotyping using 20 microsatellite loci are
81 described elsewhere [10]. Pairwise relatedness was calculated following Lynch and Ritland [12] and
82 parentage was assigned using Cervus [13]. As female group-members usually give birth
83 synchronously, all visibly pregnant females present in the group when a litter was born were
84 considered potential mothers. Due to the relatively small numbers of candidate mothers (mean = 4.3
85 per pup), maternities were assigned first. Paternity was then assigned to all pups assigned maternity
86 at $\geq 95\%$ confidence. Potential fathers included all males in the population over 1 year old at litter
87 conception (approximately 60 days before birth, mean = 72.5 candidate fathers per pup). A total of
88 629 pups were assigned paternity at $\geq 95\%$ confidence ($\geq 90\%$ confidence after taking into account
89 the probability of misassigning maternity). For 516 of these pups from 12 groups, the mother's
90 group of birth was known, allowing us to investigate whether dispersal influenced female
91 reproductive behaviour. See supplementary material for further details on sample sizes. Coefficients
92 of inbreeding were calculated using Pedantics [14] and inbreeding was quantified following [15].

93 *Statistical analysis*

94 Statistical analyses were conducted in R.3.0.1 using the lme4 package [16]. General linear
95 mixed models (GLMMs) were constructed to test whether inbreeding is more frequent (1) among
96 natal females than dispersed females; (2) among females that mate with resident rather than extra-
97 group males; and (3) in older and smaller social groups.

98

99 Results

100 Of a total of 516 pups, 328 (63.6%) were born to females that conceived within their natal
101 group to resident males (figure 1). A further 93 pups (18.0%) were born to females who remained in
102 their natal group but conceived to an extra-group male, and 95 pups (18.4%) were born to females
103 that dispersed out of their natal group (figure 1). A significantly larger proportion of pups were
104 fathered by extra-group males when females stayed within their natal group (93 of 421 pups) in
105 comparison to females that dispersed (8 of 95 pups; binomial proportions test: $\chi^2=8.35$, df=1,
106 $p=0.0039$), suggesting that natal females may sometimes mate extra-group to avoid inbreeding.

107 Relatedness coefficients calculated from microsatellite data [12] revealed that females
108 breeding within their natal group conceived to closer relatives than females that either bred with
109 extra-group males or dispersed (GLMM: $\chi^2_{(3)}=35.74$, $p=8.47 \times 10^{-8}$, figure 2, table S1). A substantial
110 proportion of females that bred within their natal groups conceived to close relatives; 26.71%
111 conceived to a male related by ≥ 0.25 and 7.53% conceived to a male related by ≥ 0.5 . The equivalent
112 proportions for females that did not breed within their natal group were substantially lower at 4.46%
113 and 0.89% respectively.

114 After excluding extra-group paternities, the mean relatedness of parent-pairs increased
115 significantly with group age (GLMM: $\chi^2_{(1)}=6.23$, $p = 0.013$, Table S2) indicating that inbreeding is more
116 likely to occur in older social groups. There was no evidence for inbreeding being more prevalent in
117 smaller groups (GLMM: $\chi^2_{(1)}=0.25$, $p = 0.62$, Table S2).

118 Pedigree assignment identified 30 individuals from four social groups with non-zero
119 inbreeding coefficients (f). These comprised 11 cases of close inbreeding ($f = 0.25$), seven cases of
120 moderate inbreeding ($f = 0.125$) and 12 cases of weak inbreeding ($0 < f < 0.125$, Table S3).

121

122 **Discussion**

123 We provide evidence that inbreeding is a regular part of the breeding system of banded
124 mongooses in our study population. The majority of pups were born to females reproducing within
125 their natal groups and, of these, a substantial proportion were conceived to relatives. A high level of
126 inbreeding was also supported by the pedigree data, which revealed close inbreeding ($f=0.25$) in 8.5%
127 of cases and moderate inbreeding ($0.25 < f \geq 0.125$) in 16.7% of cases.

128 Similar rates of moderate inbreeding have been documented in other cooperative mammals,
129 including black tailed prairie dogs (26%, [17]) and meerkats (15%, [18]). However, close inbreeding is
130 far less common and appears to be actively avoided in almost all species [5]. The unusually high rate
131 of close inbreeding in the banded mongoose could be a consequence of group structure, as we
132 found that inbreeding was more common in older social groups. This is probably due to natal
133 philopatry leading to an increasing encounter rate between opposite-sex relatives over time since
134 groups formed [10].

135 While all group members could potentially inbreed in older social groups, some categories of
136 inbreeding appear more common than others. For example, we recorded 8 instances of incest
137 between fathers and daughters (of a possible 160 observations, Table S3) but none between
138 mothers and sons (of a possible 170 observations), a highly significant difference (Binomial
139 proportions test, $\chi^2 = 6.73$, $p = 0.0095$). This may be because female banded mongooses begin
140 breeding at 1 year but males rarely reproduce until they are 3 or 4 years old [8]. Young females may

141 therefore have a high risk of encountering their fathers, while breeding males are unlikely to
142 encounter their mothers, who have since died.

143 In other mammals where females are likely to encounter their father, females either
144 disperse from their natal group prior to breeding, or mate extra-group [2]. Although both of these
145 strategies are effective at avoiding inbreeding in the banded mongoose, the majority of females
146 mated within their natal group. Why, therefore, don't all females outbreed? Theory predicts that
147 regular inbreeding may occur under circumstances where the costs of inbreeding are outweighed by
148 the costs of inbreeding avoidance [6]. It is possible that banded mongooses may have particularly
149 high costs of dispersal, since members of newly-founded groups suffer an annual adult mortality rate
150 (0.33) almost three times that of resident groups (0.12) [8]. Similarly, violent encounters between
151 neighbouring groups mean that extra-group mating risks injury [8]. Hence, there might be a net
152 benefit, at least to some females, of breeding within the natal group. Alternatively, inbreeding may
153 be tolerated if the costs of inbreeding depression are relatively low. For example, (allo)parental
154 investment towards inbred offspring could potentially buffer any fitness costs of inbreeding [3].
155 These possibilities will be the subject of future study.

156 How animals balance the costs of inbreeding and inbreeding avoidance is important to
157 understand as this can be a fundamental determinant of patterns of dispersal, reproductive skew
158 and cooperative interactions [5]. In the majority of cooperatively breeding vertebrates, the balance
159 seems tipped towards inbreeding avoidance, at least at the within-group level. Identifying species
160 where inbreeding is a normal part of the mating system will allow us to investigate how this balance
161 can be reversed, and to understand inbreeding in the context of cooperation and conflict within
162 social groups.

163

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170

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- 214

215

216 Figure 1. The frequency of within-group and extra-group paternity among the offspring of females
217 breeding (i) in their natal group, and (ii) after dispersal to a new group.

218

219 Figure 2. Mean (\pm 95% confidence intervals) relatedness values of banded mongoose breeding pairs
220 depending on whether females bred in their natal group or after dispersal, and with a resident or
221 extra-group male. The 216 breeding pairs included here produced 516 pups.



