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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°12'S; 29°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 ≥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 ≥95% confidence (≥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: χ^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=8.47x10^{-08}, 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≥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, χ^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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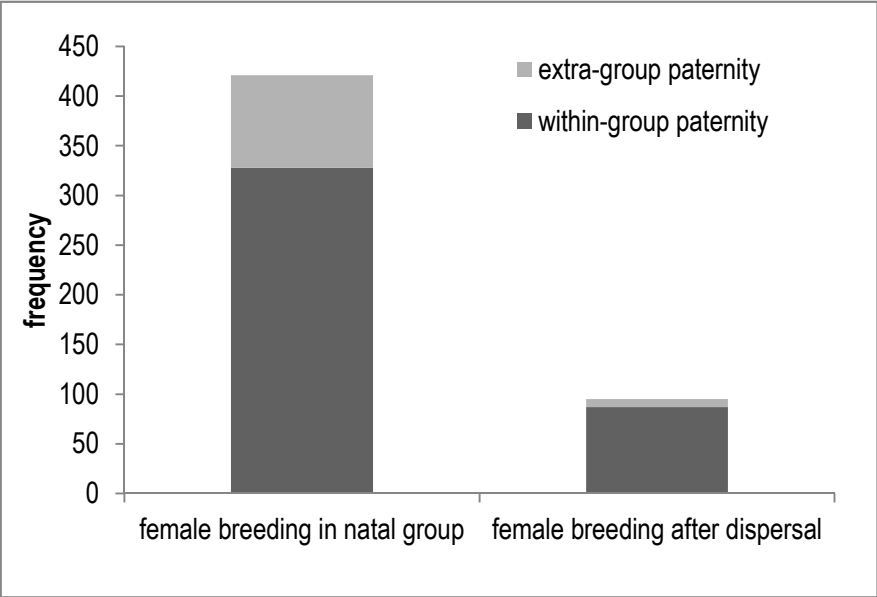189   *Ecology and Sociobiology* **57**,119-131.

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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 (± 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.