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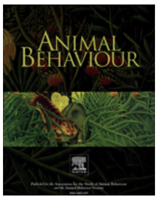

Inbreeding avoidance behaviour of male bank voles in relation to social status

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Since inbreeding can result in reduced offspring fitness, female animals often avoid mating with close relatives. In theory, males may also avoid inbreeding under certain conditions, notably if alternative mating opportunities are available at low cost. Hence competitively successful or dominant males may be more likely to avoid inbreeding because they have more mating opportunities. We tested these predictions in a promiscuous rodent with clear male dominance relationships, the bank vole, *Myodes glareolus*. Specifically, we quantified behavioural responses in relation to sibling and nonsibling females presented simultaneously under controlled experimental conditions. Male bank voles spent significantly less time in proximity to sibling than nonsibling females. However, contrary to theoretical predictions, male preference for nonsibling females did not differ significantly according to social status. Additionally, we found that male bank voles showed no preference for females as a function of either their body mass or age. Our findings suggest that regardless of their social status, male bank voles find nonsibling females more attractive than siblings. We discuss these results in relation to recent evidence of male status-dependent mate choice.

Inbreeding can result in reduced offspring fitness owing to an increase in the expression of homozygous deleterious recessive alleles (partial dominance) or to the loss of heterozygous benefits (overdominance; reviewed in Charlesworth & Willis 2009). Inbreeding avoidance behaviour may therefore be favoured to maximize reproductive fitness, despite potential inclusive fitness benefits of mating with relatives (Parker 1979; Lehmann & Perrin 2003). There is widespread evidence that female animals often favour unrelated partners, with preferences expressed via pre- and/or postcopulatory processes (Pusey & Wolf 1996; Tregenza & Wedell 2000; Pizzari et al. 2004; Hoffman et al. 2007; Ala-Honkola et al. 2010). By contrast, because males typically have higher potential reproductive rates than females and encounter sexually receptive mates less frequently, they are generally expected to be more tolerant of inbreeding, potentially resulting in sexual conflict over mating decisions (Parker 1979, 2006). However, males may also exhibit inbreeding avoidance behaviour under certain circumstances, for example if encounter rates with sexually receptive females are relatively high and/or search costs are low (Parker 1979, 1983, 2006; Kokko & Ots 2006). To date though, there have been relatively few empirical tests of male inbreeding avoidance behaviour and findings vary across taxa (Thünken et al. 2007; Lihoreau et al. 2008). For example, male pine voles, *Microtus pinetorum*, are reported to show a preference for nonsibling females compared to siblings (Solomon & Rumbaugh 1997) but red junglefowl males, *Gallus gallus*, invest more sperm when mating with related females, potentially to counteract female responses to inbreeding (Pizzari et al. 2004).

The likelihood of successful copulations between close relatives can also be determined by factors influencing within-sex variation in inbreeding tolerance. For example, in common lizards, *Lacerta vivipara*, female inbreeding tolerance is age dependent, with younger and older females more tolerant than those of intermediate age (Richard et al. 2009). Variation in the degree of inbreeding tolerance may also be expected in males, although male mate preferences are generally less well studied than those of females (Dewsbury 2005). For example, males that are able to monopolize the best areas for access to mates, or are preferred by females as mates, are likely to experience relatively low search costs and high encounter rates with sexually receptive females (Cowlishaw & Dunbar 1991; van Noordwijk & van Schaik 2004); they may therefore be expected to be more discriminating than less competitively successful males (Fawcett & Johnstone 2003; Härdling et al. 2008). In species in which male social status correlates with access to sexually receptive females, we therefore predict that dominant males should be less tolerant of inbreeding than subordinates because they generally have lower search costs and more mating and/or fertilization opportunities (Parker 2006).

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We tested these predictions in the bank vole, *Myodes* (formerly *Clethrionomys*) *glareolus*, a promiscuous small mammal. Inbreeding reduces reproductive fitness in this species (Kruczek 2007) and costs of inbreeding may explain why adult male bank voles disperse long distances compared to females (Kozakiewicz et al. 2007), although habitat constraints can limit this dispersal (Kozakiewicz et al. 2009a). Mechanisms of kin recognition may thus function to avoid costs of inbreeding in natural populations; it has been shown for example that female bank voles prefer the odour of unrelated males (Kruczek & Gołas 2003; Kruczek 2007), apparently via a mechanism of phenotype matching, since the odours of unfamiliar and unrelated males are preferred over those that are unfamiliar and related (Kruczek 2007). Male bank voles establish clear dominance relationships based on aggressive behaviour and scent signalling (Rozenfeld et al. 1987; Kruczek 1997) and dominant males achieve higher reproductive success than subordinates in both pre- and postcopulatory competition (Horne & Ylönen 1996; Klemme et al. 2006). We thus predicted that dominant males would have a lower inbreeding tolerance than subordinate males, owing to their greater fertilization opportunities (Parker 2006).

METHODS

Subjects and Housing

Subjects used in this experiment were captive born from wild-caught animals. The breeding colony of bank voles from which subjects originated was founded using 29 wild-caught individuals (15 males and 14 females). We captured these animals in Cheshire (U.K.) using Longworth traps containing food (LabDiet 5002 and apple pieces) and paper-wool nest material. Traps were laid down in the evening (1800 hours), checked the following morning (0830 hours) and opened in the laboratory. The colony was maintained at the University of Liverpool to provide animals for several experiments. These animals were kept under laboratory conditions in MB1 cages (45 × 28 cm and 13 cm high, North Kent Plastic Cages Ltd., Rochester, U.K.). Food (LabDiet 5002) and water were provided ad libitum. Animals were maintained on a reversed photoperiod (light:dark 16:8 h, lights on at 1700 hours), and at a temperature of 21 ± 1 °C. After weaning, when individuals were 21 days old, they were housed with siblings of the same sex in MB1 cages containing substrate (Corn Cob Absorb 10/14 substrate) and paper-wool nest material. Females were housed individually in M3 cages (48 × 11.5 cm and 12 cm high, North Kent Plastic Cages Ltd) to avoid mixing their odours prior to experimental tests. Hence, at the start of the experiments, all same-sex individuals had equivalent social experience and none had previously mated. For purposes of identification, male subjects were PIT tagged just below the neck (tag length 12 mm and diameter 2.12 mm; UKID Systems, Preston, U.K.). None of these animals has shown any evidence of adverse effects after being tagged. On the day of the first trial, females were aged between 9 and 46 weeks and weighed between 14.9 g and 25.2 g; male subjects were aged between 12 and 32 weeks and weighed between 16.2 g and 32.9 g. At the end of the experiment, all individuals were returned to the stock population. This research adhered to the legal requirements of the country in which the work was carried out and all institutional guidelines. No specific licences were required.

Establishing Dominance Relationships

We set up 30 pairs of nonsibling males in MB1 cages divided in two by a mesh barrier with one male of each pair housed in each part of the cage (i.e. in an area of 45 × 14 × 13 cm). This separation allowed continuous olfactory, visual and auditory contact between males while they were housed together.

To assess scent-marking behaviour and assign social status to subjects, both males from a pair were transferred to clean Benchkote-lined MB1 cages (again divided in two by a mesh barrier) and left for 30 min during the dark phase. Scent marks were scanned using a Bio-Rad Fluor-S MultiImager (QuantityOne software: 12 s exposure, 530DF60 Filter, UV light source Epi illumination, high-resolution mode; Bio-Rad Laboratories, Hemel Hempstead, U.K.). The social status of the males was assessed based on the criteria identified by Rozenfeld & Rasmont (1991; see also Horne & Ylönen 1996). Specifically, thin streaks of urine deposited throughout the arena are characteristic of dominant males. By contrast, subordinates either deposit large pools of urine, especially in corners of the arena (Rozenfeld et al. 1987; Rozenfeld & Rasmont 1991; Klemme et al. 2006), or they deposit no urine marks (Rozenfeld & Rasmont 1991). Nest material (approximately 13 g) from a nonsibling female was added once to each compartment of the divided cages, 1 day prior to the first collection of scent marks from each male pair to increase male competitiveness (Kruczek 1997). Male roles of dominant and subordinate were assigned when a clear and consistent difference in the pattern of scent marks within a pair was apparent for three successive scent-marking assays (each conducted at least 24 h apart). Males were then kept paired until the end of the experiment. If no clear dominant–subordinate pattern could be identified within a pair, males were rehoused in their original cages or paired with a new nonsibling male. There was no difference in body mass between dominant and subordinate males (dominants: $\overline{X} = 23.5 \pm 0.7$ g; subordinates: $\overline{X} = 23.2 \pm 0.9$ g; $t_{26} = 0.76$, $P = 0.77$).

Quantifying Inbreeding Avoidance Behaviour

To assess male behaviour, we used a choice chamber consisting of three interlinked MB1 cages. A central (neutral) cage was linked via tunnels (3 cm diameter) to two adjacent cages. Each adjacent cage was divided in two by a mesh barrier, thus overall forming one large central chamber and two smaller outer chambers. During behavioural tests, subject males were placed in the central chamber, and a female placed in each of the two outer chambers. This allowed the male visual, auditory and olfactory contact with potential mates. The day before the experiment, males were habituated to this experimental apparatus for 30 min with female nest material (approximately 30 g) in the two outer cages to expose each male to female odours. The apparatus was cleaned between each trial and female odour samples used for this prior exposure were taken from the stock population rather than from females that the male would encounter in the experiment.

To test whether male bank voles show greater interest in nonsibling than in sibling females, and whether this response varies according to social status, we offered 28 males of known dominance status simultaneous access to a sister and a nonsibling female. Positions of related and unrelated females were balanced between the two adjacent cages. Dominant and subordinate males from the same pair were tested with the same females, such that one female was a sibling of the dominant and one female was a sibling of the subordinate. In most cases (22/28 males), sisters were full siblings selected from a different litter from the subject male (hereafter called unfamiliar siblings). Owing to limited availability of unfamiliar siblings, sisters were taken from the same litter for the remaining six males (hereafter called familiar siblings). In such cases, males and females had been housed together until weaning (approximately 22 days). Females ($N = 17$) were used with one or two pairs of males but when used twice, the second female of the pair was always different. We recorded male behaviour for a period of 30 min, commencing after the male had visited each female cage once and had returned into the central cage. DVD recordings were analysed to quantify the time that subject males spent in each female's cage and the number of visits to each cage.

Statistical Analysis

Normality of the data was tested by Kolmogorov–Smirnov tests and log transformations were applied when necessary. Paired *t* tests compared the time spent by males in nonsibling and sibling female cages, and the number of visits to these cages. We counted a visit only when the male's entire body was inside the female's cage. To test simultaneously for an effect of female relatedness and female familiarity, we employed a general linear model (GLM) including 'relatedness' and 'familiarity' as fixed factors and time in the left-hand cage minus time in the right-hand cage as the outcome variable. Similarly, to test simultaneously for an effect of female relatedness and male dominance status on the time that males spent in each female cage, we employed a GLM including 'relatedness' and 'male dominance status' as fixed factors and time in the left-hand cage minus time in the right-hand cage as the outcome variable. This approach allowed us to test simultaneously for effects of both factors, but treats males as independent with respect to their social status even though they were paired to establish dominance relationships. Therefore, paired *t* tests were conducted as complementary analyses in which male subjects within each pair were not regarded as independent. Here we compared the proportion of time that males spent in the cage of the nonsibling female. In addition to the main test for an effect of female relatedness on male behaviour, we also tested for putative effects of female age or mass on male behaviour. To avoid pseudoreplication, we used the percentage of time that both males from the same pair spent in female cages. All tests are two tailed and were conducted using SPSS 18.0 (SPSS Inc., Chicago, IL, U.S.A.). Data are presented as means ± SEM and differences are regarded as statistically significant at $P < 0.05$.

RESULTS

When male bank voles were offered simultaneous access to sibling and nonsibling females, they spent significantly less time visiting siblings than nonsibling females (Fig. 1, Table 1), although there was no significant difference in the number of visits to the cages of these females (Table 1). The tendency of male bank voles to spend less time visiting sibling females appears to be independent of familiarity, as only 'relatedness' explains the time that males spent in each cage (GLM: relatedness: $F_{1,25} = 7.04$, $P = 0.014$; familiarity: $F_{1,25} = 1.74$, $P = 0.20$). Male age had no influence on the proportion of time spent in the cage of the nonsibling female (Pearson correlation coefficient: $r_{26} = 0.02$, $P = 0.92$).

We next tested for an influence of male social status on the time spent visiting female cages, and found no evidence for an interaction with female relatedness (GLM: male dominance status*-relatedness: $F_{1,24} = 0.01$, $P = 0.91$); hence it appears that male preference for nonsibling females is not influenced by dominance status. Similarly, paired *t* tests between dominant and subordinate males reveal that the proportion of time spent in the cages of nonsibling females was not influenced by male dominance status (Fig. 2, Table 1), and the percentage of visits to cages of nonsibling females also did not differ significantly according to male social status (Table 1).

Finally, we tested a posteriori for additional putative factors (female age and female body mass) that might affect male behaviour. We found no evidence that these were likely to have an impact on mate choice, since males did not show any significant difference in the percentage of time they spent visiting cages according to female age (youngest: $\overline{X} = 44.74 \pm 4.66\%$; oldest: $\overline{X} = 55.26 \pm 4.66\%$; $t_{12} = -1.13$, $P = 0.28$) or body mass (lightest: $\overline{X} = 47.29 \pm 4.51\%$; heaviest: $\overline{X} = 52.71 \pm 4.51\%$; $t_{13} = -0.60$, $P = 0.56$).

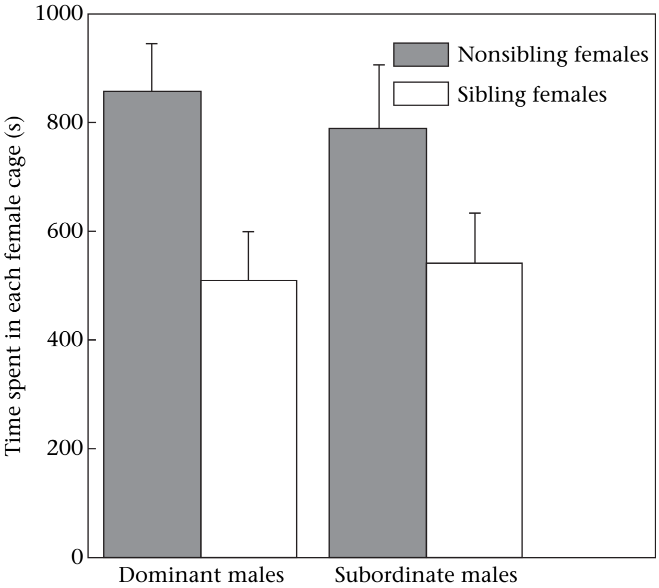

Figure 1. Time spent by male bank voles in the cages of nonsibling and sibling females. Error bars represent mean ± SEM.

DISCUSSION

When male bank voles in our study were offered simultaneous access to sibling and nonsibling females, they spent significantly less time in proximity to siblings. If the time spent in proximity to females reflects male sexual interest, our findings indicate that male bank voles may be less likely to pursue copulation attempts with sisters than with nonsibling females. These findings are consistent with previous evidence of male inbreeding avoidance in rodents (e.g. Bolhuis et al. 1988; Solomon & Rumbaugh 1997), including bank voles. For example, Kruczek & Gołas (2003) found that male bank voles switch from exhibiting a preference for their mother to a preference for nonsibling females when they become sexually mature. Similarly, adult male common voles, *Microtus arvalis*, pine voles, and laboratory mice, *Mus musculus*, have been reported to show a preference for nonsibling females compared to siblings (Barnard & Fitzsimons 1988; Bolhuis et al. 1988; Solomon &

Table 1
Comparison of how male bank voles of known dominance status behave when offered a simultaneous choice of sibling and nonsibling females

		N	Sibling female	Nonsibling female	*t*	*P*
Time (s)	All males	28	525.9±62.1	822.6±71.1	−2.50	0.02
	Dominants	14	509.6±88.0	857.5±85.0	0.85	0.41
	Subordinates	14	542.2±90.9	787.7±116.6		
Visits	All males	28	10.6±1.0	10.0±1.3	−0.76	0.45
	Dominants	14	10.6±1.3	10.6±2.0	0.6	0.56
	Subordinates	14	10.5±1.7	9.5±1.5		

To test for an overall male preference according to female relatedness, we first compared, using paired *t* tests, the absolute time spent by males in cages of sibling versus nonsibling females and the number of visits made to each of their cages. Then to test whether dominant and subordinate males responded differently, we used paired *t* tests on the percentage of time spent by males in nonsibling female cages and percentage of visits made to nonsibling female cages (see Methods). All results are presented as mean ± SEM.

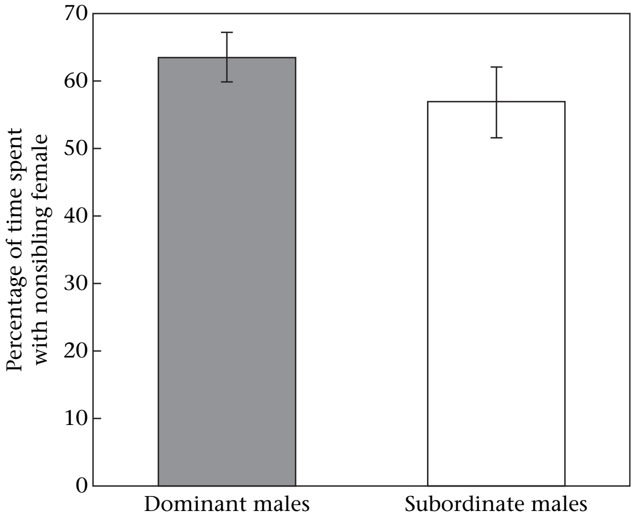

Figure 2. Time spent by dominant and subordinate male bank voles in the cages of nonsibling and sibling females. Error bars represent mean ± SEM.

Rumbaugh 1997). Results sometimes differ according to the stimuli used in these experiments (see Barnard & Fitzsimons 1988), but generally suggest that male subjects are responding to cues of relatedness rather than to the behaviour or relative receptivity of females. For example, male bank voles prefer nonsibling females to siblings when these females are anaesthetized (Kruczek & Gołas 2003), and similar findings for common and pine voles are based on male preference for female odour cues (Bolhuis et al. 1988; Solomon & Rumbaugh 1997). Limited evidence from our own study suggests that such discrimination by male bank voles may be based on phenotype matching (Kruczek 2007), since male preference for nonsibling females was independent of familiarity. In natural populations, male bank voles may regularly encounter unfamiliar relatives, including both full and half-siblings, because of high levels of promiscuity (Klemme et al. 2008), and previous studies demonstrate evidence of discrimination between related and unrelated individuals independent of familiarity (Kruczek & Gołas 2003; Kruczek 2007; Kozakiewicz et al. 2009b). Our findings are consistent with these results, and add to growing evidence of genetic mechanisms of kin recognition in rodents and other mammals (e.g. Cheetham et al. 2007; Widdig 2007; Boulet et al. 2010).

We investigated for the first time in a mammal whether inbreeding avoidance behaviour differs in relation to male social status. However, we found no significant difference between dominant and subordinate male bank voles in their preference for nonsibling females, suggesting that inbreeding avoidance behaviour may occur regardless of social status. Theoretical predictions suggest that in situations of high male competition, disfavoured competitors should be less choosy than favoured competitors (Fawcett & Johnstone 2003; Härdling et al. 2008) and these predictions have recently found some support. Specifically, Candolin & Salesto (2009) found that male three-spined sticklebacks, *Gasterosteus aculeatus*, showed a preference for larger females but that when mating competition increased, only males in good condition continued to prefer larger females whereas those in poor condition became indiscriminate. To date, evidence for variation in overt inbreeding avoidance behaviour according to differences in male social status remains limited. However, since we conducted our experiment in a simultaneous choice design we cannot rule out the possibility that dominant and subordinate males might behave differently in a sequential choice situation (Barry & Kokko 2010). In addition, it is possible that dominant and subordinate males may vary their sperm allocation strategies differently according to female relatedness, since it is known that rodents are able to adjust sperm allocation in other contexts (e.g. according to variation in the risk or intensity of sperm competition, delBarco-Trillo & Ferkin 2006).

Male bank voles in this study showed no preference for females as a function of either their body mass or age, which contrasts with recent findings in other species such as fiddler crabs, *Uca mjoebergi* (Reading & Backwell 2007) and chimpanzees, *Pan troglodytes* (Muller et al. 2006). However, while female body size and age may often reflect fecundity (and therefore reproductive value), and thus could form the basis for adaptive male mate choice (Bonduriansky 2001; Xu & Wang 2009), in bank voles evidence that female body mass correlates with litter size is mixed (Koskela et al. 1997; Klemme et al. 2006) and there is to our knowledge no report of a decrease in female reproductive success with age (at least over the range considered here).

In conclusion, our findings suggest that regardless of their social status, sexually mature male bank voles find nonsibling females more attractive than siblings. However, we suggest that further studies should consider variation in male phenotype to explain mismatches between theoretical predictions and empirical evidence in studies of inbreeding avoidance behaviour (Kokko & Ots 2006).

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