

Does it pay to be a dominant male in a promiscuous species?

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In many species male dominance leads to an increased access to mates through male-male competition and/or female choice. However, for promiscuous species, in which both males and females mate several times with different partners, male mating success is not necessarily correlated with male reproductive success. We conducted an enclosure study on the promiscuous bank vole (*Clethrionomys glareolus*) to investigate the influence of male social status on reproductive success. We assessed male dominance in the laboratory from urine marking behavior. Thereafter, we released male pairs of either a clearly different dominance relationship or an equal dominance along with four unrelated females to outdoor enclosures for 10 to 12 days and followed their reproductive output. On average 2.1 females per enclosure were breeding, i.e. the mean operational sex ratio was 1. Paternity analyses revealed no correlation between male dominance and reproductive success. Male body mass, which was not correlated to social status, was also not related to reproductive success. We suggest that, in bank vole males, sexual selection for dominance or body mass may not be strong. The benefit of multi-male mating in promiscuous species may therefore override the benefit of mating with high quality males.

Introduction

For species in which maternal investment exceeds paternal investment, sexual selection

theories predict that males can increase their reproductive success by increasing their number of mates, whereas females can increase their reproductive success primarily by increasing the

quality of their mates (Trivers 1972, Clutton-Brock & Vincent 1991). In males, this leads to the evolution of sexually selected traits that increase success in competition over mates (intrasexual selection) and traits that signal quality and are important for mate choice processes (intersexual selection) (Darwin 1871, Andersson 1994). In many mammals, social dominance of males has been shown to increase access to females by male-male competition and/or female choice, although this concept cannot be generally applied (Dewsbury 1982, Ellis 1995). Dominance of one individual over one or more other individuals results from a stable asymmetry in agonistic behaviors, leading to differential access to resources (Dewsbury 1982). The outcome of such agonistic behaviors often is determined by morphological and behavioral traits (Ellis 1995, Qvarnström & Forsgren 1998). In rodents, olfactory signals are the common mode for communication and high levels of scent-marking are associated with the maintenance of dominance amongst males (e.g. Desjardins *et al.* 1973, Brinck & Hoffmeyer 1984, Rozenfeld *et al.* 1987, Rozenfeld & Rasmont 1991, Hurst 1993). Traits that indicate and maintain social dominance may be costly because they can increase the level of energetic stress, predation risk or disease susceptibility (Qvarnström & Forsgren 1998). In fact, recent studies (e.g. Gosling *et al.* 2000 on house mouse) demonstrated costs of signaling male dominance, implying that it is a reliable and cheat-proof signal which should be favored by sexual selection (Zahavi 1975). Females should therefore choose to mate with dominant males because they may gain good genes for their offspring, but also access to high quality resources (Kirkpatrick & Ryan 1991). Indeed, many studies on rodents have shown a positive correlation of male dominance and mating success, including both studies based on female choice (Huck & Banks 1982, Shapiro & Dewsbury 1986, Horne & Ylönen 1996) and studies that include male-male competition (Dewsbury 1981, Huck & Banks 1982, Lisk & Baron 1983, Wolff 1985, Wynne-Edwards & Lisk 1988).

Strong sexual selection for traits indicating male dominance is intuitive for species with sexually polygynous mating systems. However, in

species with sexually promiscuous mating systems, females are not monopolized by a single male and subordinate males may also gain success in mating. In such mating systems, male reproductive success is therefore also a function of post-copulatory strategies, i.e. sperm competition and cryptic female choice (Ginsberg & Huck 1989, Eberhard 1996). It is thus unclear if male dominance is correlated with male reproductive success in promiscuous species (Dewsbury 1982).

The bank vole (*Clethrionomys glareolus*) is a common arvicoline species with a promiscuous mating system. *Clethrionomys* species show a clear social organization. Breeding females are solitary and territorial (Bujalska 1990). Mature males form stable dominance hierarchies and have large home ranges, which overlap each other as well as those of several females (Viitala 1977, Viitala & Hoffmeyer 1985, Bujalska 1990). Laboratory experiments showed that bank vole females gain indirect benefits from mating with dominant males. Male traits reflecting dominance, weight of preputial glands and urine marking behavior, have high heritabilities (Horne & Ylönen 1998). Further, male dominance has a significant effect on offspring size at birth and growth until weaning (Horne 1998) and both traits appear to affect female maturation (Koskela 1998) and reproductive success (Ylönen *et al.* 2004). Horne and Ylönen (1996) also showed that bank vole females were able to distinguish males of different social status and preferred dominant over subordinate males. However, in their study, only a female's first mating choice was observed. Since bank vole females commonly mate with multiple males during one estrus cycle and paternity does not depend on mating order (Ratkiewicz & Borkowska 2000), the mating success of dominant males in the first choice does not necessarily correlate with reproductive success.

Our aim was to study the influence of male dominance on male reproductive success in bank voles under semi-natural conditions. We assessed male dominance in the laboratory from urine marking behavior. Thereafter, we conducted a field experiment in outdoor enclosures and compared the reproductive success of high ranking males in two competitive situations: together

with a subordinate male and together with a male of a similar high social status.

Material and methods

Study animals

Most of the animals used in the experiments were the F1 generation of wild caught individuals originally captured at Konnevesi, central Finland (62°37'N, 26°20'E). Only part of the males was wild caught. They were trapped as weanlings about eight months prior to the experiment and were housed in the laboratory until the experiment started. We therefore assumed that the different origin of our experimental males did not introduce an artifact. The animals were housed in standard mouse cages (43 × 26 × 15 cm) with wood shavings and hay as bedding and food and water available *ad libitum*. Males and females were kept in groups of two individuals of the same sex in each cage. The temperature in the laboratory remained constant at 23 ± 1 °C and a 18L:6D illumination cycle was maintained. All voles were marked with small mammal ear tags for individual recognition.

Male dominance estimation

Male dominance was assessed in paired trials by observing urine marking behavior. The marking behavior of dominant and subordinate bank vole males is known to be different: dominant males cover large areas of substrate with urine marks in the form of fine traces, whereas subordinate males stop marking in the presence of dominant males and deposit only concentrated spots of urine in a few locations (Rozenfeld & Rasmont 1991, Horne & Ylönen 1996). Assessing dominance relationships of bank vole males on the basis of their urinary behavior is a reliable method and is preferable to forcing direct encounters because injuries can be avoided by the prevention of physical contact (Horne & Ylönen 1996).

All males were seven to ten months old and of proven fertility as indicated by having sired at least one litter prior to experimentation. In the

testing procedure two randomly chosen males were weighed and kept overnight for 12 hours in a 60 × 40 × 34 cm bottomless arena with food and water available. The arena was divided into two equal-sized compartments by a wire mesh. One male was kept in each compartment to guarantee spatial separation, but to allow visual, acoustic and olfactory contact. Brown paper was placed under the arena to collect urine marks. Urine stained the paper pale and left clear visible traces. After each trial the arena was cleaned with water and ethanol and the paper was renewed.

The dominance relationship of two males was determined by calculating the percent coverage of fine trace urination marks by placing the urine marked paper under a transparent grid. Males that differed in their percent coverage by more than 50% were regarded as pairs with different dominance relationship. The mean percent coverage of dominant males was 90% (range 85%–100%) and of subordinate males 35% (range 30%–40%). If the difference of marked area was not larger than 20% males were regarded as equally dominant. Both individuals in equal male pairs showed high percentages of coverage (80%–100%).

Altogether we tested 86 males in 66 dyads, i.e. some of the males were tested against two males. Of these 66 male pairs, 33 could be assigned to one of the two dominance categories, i.e. clearly different or equally dominant. These male pairs were tested again within seven days and we found that 27 of 33 male pairs (81%) showed the same urination pattern in both tests. Male pairs whose dominance relationship could not be determined unequivocally after two tests were not used in the study. For the field experiment we used the same male pairs as in the dominance tests and chose from the 27 pairs 12 male pairs with a clearly different dominance relationship and 8 male pairs with a relationship of similar dominance.

The marking behavior of a male remains constant over long periods of time in the laboratory (Horne & Ylönen 1998). To test whether the estimated dominance relationship of two males remained stable during the experiment we re-tested six of the 20 male pairs (four pairs of different dominance and two pairs of equal dominance) after experimentation. We found that the

dominance hierarchies of all six pairs remained constant and no dominance reversals occurred. The mean difference in percent coverage of fine trace urination marks of four different dominance pairs remained relatively constant with 70.0% before the experiment and 70.3% after the experiment. Two male pairs of equal dominance showed a moderate change towards a more equal direction from 20.0% to 10.0%.

Dominant and subordinate males did not differ in body mass (mean_{dom} $\pm$ SD = 23.9 $\pm$ 5.8 g, mean_{sub} $\pm$ SD = 24.1 $\pm$ 3.9 g, paired *t*-test, *n* = 12, *t*₁₁ = -0.088, *p* = 0.931). We also found no difference in body mass between males of equal dominance status (mean_{equal 1} $\pm$ SD = 22.8 $\pm$ 2.9 g, mean_{equal 2} $\pm$ SD = 22.6 $\pm$ 2.6, *n* = 8, *t*₇ = 0.216, *p* = 0.836).

Enclosure experiment

The enclosure experiment was conducted in July and August 2000 in eight 0.25 ha outdoor enclosures situated in an abandoned field at Konnevesi Research Station, central Finland. The enclosures were fenced with 1.5-m-high galvanized sheet metal which was embedded 0.5 m into the ground to prevent the escape of animals. We released two males of known dominance relationship, either different or equal, and four nulliparous females (19–25 days old), into each enclosure. Each enclosure allows up to four females (mean = 3.2) to establish territories and breed simultaneously (Eccard *et al.* 2002). All individuals of an enclosure were unrelated to each other. Each enclosure held a grid of 25 multiple-capture live traps (Ugglan Special) at regular intervals of 10 m. After an initial period of three days of habituation, survival of the animals was monitored by live trappings. The traps were activated in the afternoon at 17:00 and checked in the evening at 21:00 and the following morning at 09:00. After the morning check, traps were deactivated for one day, one night and the following day until activated again in the afternoon. In this way survival was followed every day, but the voles were free to move and interact two thirds of the time. The trappability of bank voles in this experiment was 78%, i.e. we trapped on average 4.7 (range 2–6) out of the six individu-

als per enclosure and trapping event. After ten to twelve days, all animals were trapped and brought to the laboratory. We housed females in separate cages and recorded the number and the date of birth of offspring. In total we obtained data on 20 groups of bank voles, 12 replicates with male pairs of different dominance and eight replicates with male pairs of equal dominance. Enclosure replicates were started in groups of one to four enclosures studied simultaneously. A total of 80 females and 40 males were used in the field experiment and each individual was used only once.

Paternity analyses

A tissue sample was taken from every animal involved in the experiment. A small piece of ear was cut with sterile, sharp scissors. The procedure was performed during routine handling and lasted a few seconds. We did not apply anaesthetic or antiseptic, however no adverse effects were observed. The tissue was fixed in 98% ethanol and preserved at 4 °C. DNA was extracted from the tissue samples using a standard proteinase K/chloroform method (Sambrook *et al.* 2001). Polymerase chain reaction (PCR) amplification was conducted for up to five different microsatellite loci MSCg-4, MSCg-18, MSCg-20, MSCg-24 and MSCg-31 (Gockel *et al.* 1997, Gerlach & Musolf 2000). We first typed two of these five loci. If paternity was not unambiguously shown for each single offspring with each of the two primers, we used more successive primers until paternity was proven twice for each offspring. PCR products were separated on Spreadex El 400 S 50 Gels (Elchrom Scientific, Switzerland) using electrophoresis. To determine paternity, the alleles of each pup were visually compared with those of the known mother and the two potential fathers.

Data analysis

Statistical analyses were performed using SPSS 11.0 (SPSS Inc.). We used nonparametric statistics when normality and/or homogeneity were not satisfied. Probability values are two-tailed

and the level of significance was set at $\alpha = 0.05$. In two of the replicates, one of the males did not survive the experiment. In another replicate, none of the four females were breeding. We excluded these three replicates from statistical calculations.

Because male dominance was not related to body mass (*see* male dominance estimation), the relationship of these two male traits to reproductive success was analyzed separately. Overall, mean male body mass was 23.5 g (range 18.5–38.0 g). For statistical evaluations of body mass status we included only male pairs ($n = 13$) with a minimum difference in body mass of 1.0 g (mean difference: 4.3 g, range 1.0–17.4 g). Data on male reproductive success, i.e. the proportion of offspring sired per litter, were averaged for each replicate. To avoid pseudoreplication we used information from only one male per replicate: (a) in different dominance pairs the proportion of offspring sired by the dominant male, (b) in equal dominance pairs the proportion of offspring sired by a randomly chosen male, and (c) among both treatments the proportion of offspring sired by the heavier male. This proportion was transformed into a binary variable according to whether the focus male sired more than 50% of the offspring or less than 50% of the offspring and this was analyzed by binominal tests. We used logit regression analysis to test whether the number of multiply sired litters out of the total number of litters per replicate differed between both treatments. Since the probability of multiple paternity depends on litter size (J. A. Eccard, I. Klemme & H. Ylönen unpubl. data) we included $\log_{10}$ (mean litter size of each enclosure) as a covariate.

To test whether the proportion of offspring sired depends on the operational sex ratio (number of receptive females/fertile males) we correlated reproductive success of dominant males and males of large body size with the number of breeding females in each replicate. Although some matings may not result in pregnancy, we assumed that the proportion of failed matings was even among replicates. We also calculated the day of conception for each litter based on a gestation period of 20 ± 1 days (own observation) to obtain data on breeding synchrony and correlated it to male reproductive success.

Results

General results

Altogether data from eleven replicates containing males of different dominance and six replicates containing males of equal dominance were analyzed. We found no significant difference between the treatments in the number of surviving females per replicate ($\text{mean}_{\text{diff}} \pm \text{SD} = 3.9 \pm 0.3$, $\text{mean}_{\text{equal}} \pm \text{SD} = 3.9 \pm 0.4$), the number of breeding females per replicate ($\text{mean}_{\text{diff}} \pm \text{SD} = 1.9 \pm 0.9$, $\text{mean}_{\text{equal}} \pm \text{SD} = 2.5 \pm 1.0$), the number of offspring born per replicate ($\text{mean}_{\text{diff}} \pm \text{SD} = 10.2 \pm 5.1$, $\text{mean}_{\text{equal}} \pm \text{SD} = 13.8 \pm 5.8$) and the mean litter size per replicate ($\text{mean}_{\text{diff}} \pm \text{SD} = 5.4 \pm 0.8$, $\text{mean}_{\text{equal}} \pm \text{SD} = 5.6 \pm 0.7$, Mann-Whitney U -test: $n_{\text{diff}} = 11$, $n_{\text{equal}} = 6$, $U = 32.50$, $U = 21.50$, $U = 18.50$ and $U = 26.00$ respectively, all p 's > 0.149).

Paternities of 195 offspring from 36 litters were analyzed with DNA microsatellite genetic markers. All alleles of all pups could be assigned to one of the potential fathers and the mother. Twenty four of the 36 litters were sired by a single male, and 12 litters (33.3%) were sired by both males. The proportion of multiply sired litters per replicate was not significantly influenced by treatment (logit regression analysis: $\chi^2 = 17.831$, $\text{df} = 14$, $p = 0.215$).

Male dominance and reproductive success

Dominant males sired an average proportion of 0.41 ± 0.42 (mean $\pm$ SD) offspring per replicate (Fig. 1) and only in four out of 11 replicates more than 50% of the offspring. Hence the number of replicates in which the dominant male was more successful than the subordinate male did not deviate significantly from the random expectation of 50:50 (binominal test one-tailed: $n = 11$, $p = 0.275$).

In the equal dominance treatment, a randomly chosen male sired on average 0.51 ± 0.29 (mean $\pm$ SD) offspring per replicate (Fig. 1) and in two out of six replicates more than half of the offspring (binominal test: $n = 6$, $p = 0.688$). Similarly, the proportion of replicates in which the

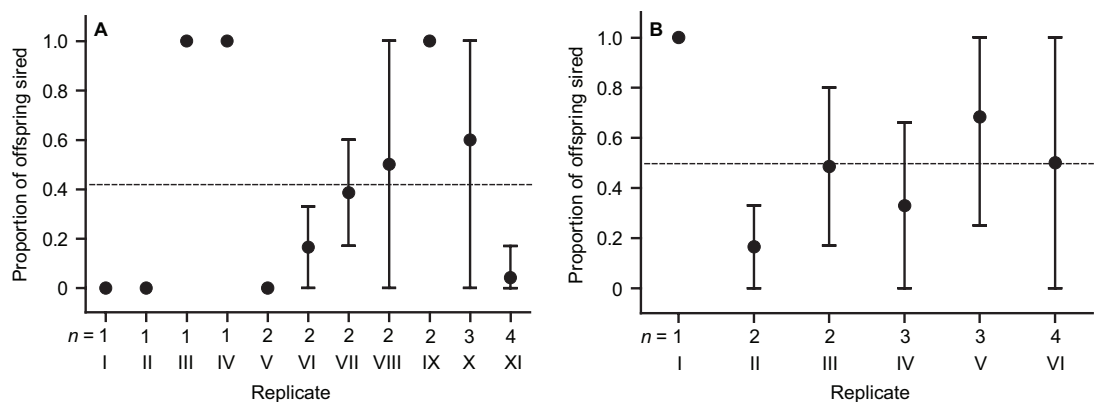


Fig. 1. Proportion of offspring sired by (A) the dominant male from the different dominance treatment and (B) a randomly chosen male from the equal dominance treatment among all replicates. Circles and whiskers represent mean and range of data, sample size represents the number of litters per replicate and the dotted line represents the overall mean among all replicates.

focus male sired more than half of the offspring did not differ from random expectation when singly and multiply sired litters were considered separately (Table 1). However, the variation in reproductive success within and among replicates varied considerably (Fig. 1).

Male body mass and reproductive success

Males of different body mass did not differ in reproductive success. The heavier male of a male pair sired only in six out of 13 replicates more than half of the offspring (mean $\pm$ SD =

0.55 ± 0.38 ; binominal test one-tailed: $n = 13$, $p = 0.500$). Thereby the proportion of offspring sired by the heavier male was not related to the actual difference in body mass between two males (Spearman's correlation: $r = 0.107$, $p = 0.727$). The proportion of replicates, in which the heavier male sired more than half of the offspring, did not differ from random expectation when analyzing singly and multiply sired litters separately (Table 1).

In four out of 11 male pairs of different dominance the heavier male was dominant, in two pairs both males were of similar body mass (< 1 g difference) and in five pairs the lighter male was dominant. The proportion of offspring sired by

Table 1. Male reproductive success among singly and multiply sired litters, including the total number of replicates in which singly and multiply sired litters occurred (n), the number of replicates in which the focus male sired more than 50% of the offspring and mean proportion $\pm$ SD of offspring sired by the focus male. P values are given for the binominal tests (one-tailed for dominance different and body mass, two-tailed for dominance equal). Note that in some replicates both singly and multiply sired litters occurred, but in other replicates only one type of litter occurred.

	Singly sired litters		Proportion of offspring sired	p	Multiply sired litters		Proportion of offspring sired	p
	n	Focus male > 50 %			n	Focus male > 50 %		
Dominance different (dominant male)	10	3	0.38 ± 0.45	0.172	4	1	0.42 ± 0.30	0.313
Dominance equal (rand. chosen male)	5	2	0.49 ± 0.50	> 0.999	4	2	0.54 ± 0.16	> 0.999
Body mass (heavier male)	11	6	0.48 ± 0.46	0.500	6	3	0.50 ± 0.22	0.500

the dominant male did not differ between male pairs in which the dominant male was heavier or lighter than the subordinate male ($\text{mean}_{\text{heavy}} \pm \text{SD} = 0.38 \pm 0.44$, $\text{mean}_{\text{light}} \pm \text{SD} = 0.40 \pm 0.41$, Mann-Whitney U -test: $n_{\text{heavy}} = 4$, $n_{\text{light}} = 5$, $U = 9.00$, $p = 0.805$).

Operational sex ratio and reproductive success

The number of breeding females per replicate was not correlated with the proportion of offspring sired by the dominant male (Pearson's correlation: $n = 11$, $r = 0.196$, $p = 0.563$) or the heavier male ($n = 13$, $r = 0.048$, $p = 0.876$). In all but three enclosures, all females were breeding synchronously, i.e. all litters of a replicate were born within three days. The maximum number of simultaneously breeding females per replicate was also not correlated to the proportion of offspring sired by the dominant male (Pearson's correlation: $n = 11$, $r = -0.179$, $p = 0.598$) or the heavier male ($n = 13$, $r = 0.010$, $p = 0.974$).

Discussion

Our results show that male dominance, assessed by urine marking behavior, and male body mass were not related to male reproductive success. Dominant and subordinate males, males of equal dominance, and males of different body mass sired on average the same proportion of offspring. Although our sample sizes are not sufficient to detect small differences in paternity outcome, our prediction was that if social dominance is favored by sexual selection, then dominant males should sire the great majority of offspring. Instead, variation in reproductive success was high among and within replicates, suggesting that reproductive success is related to traits other than social dominance. This is in contrast with two other studies on rodents, both of which showed a positive relationship between dominance rank and reproductive success (Dewsbury 1981, Keil *et al.* 1999).

Although in the laboratory female bank voles prefer to mate with dominant males first, and benefit from mating with dominant males (Horne

& Ylönen 1996, 1998, Horne 1998), in the wild they commonly mate with multiple males during one estrus cycle (Ratkiewicz & Borkowska 2000). A laboratory study, in which bank vole females were successively mated with two randomly chosen males, revealed that 35% of all resulting litters were multiply sired (T. J. Horne, I. Klemme & H. Ylönen unpubl. data). Thus, the proportion of multiply sired litters in the present study (33%) suggests that the majority of females engaged in multi-male mating. Individual male reproductive success in a multi-male mating system depends on a number of factors, including sperm quality and quantity, mating order and frequency, and timing of mating in relation to ovulation (Ginsberg & Huck 1989). These factors can be inter-related with social status and thus lead to greater reproductive success of dominant males despite multi-male mating (*see* Ginsberg & Huck 1989 for review). In laboratory mice, for example, male dominance has been found to be positively related to both sperm density and motility (Koyama & Kamimura 1999, 2000). However, little is known about the role of male dominance in sperm competition in bank voles.

Also, there is increasing evidence that females play an active role in determining paternity after multi-male mating (*see* Jennions & Petrie 2000 for review). It is unclear why females would promote paternity of subordinate males equally as often as of dominant males, but female choice may alter with environmental conditions or might be density dependent (Qvarnström & Forsgren 1998). Especially in the wild, where many uncontrollable factors influence individual behavior, female choice decisions might be different to those observed under stable laboratory conditions, where both males were offered simultaneously to the female.

A correlation between male dominance and relative body size is expected because large body size reflects competitive ability. However, studies on mice have shown that dominant males are sometimes smaller than subordinates (Gosling *et al.* 2000, Rolland *et al.* 2003). This is explained because the outcome of an agonistic interaction is partly determined by each individual's motivation to invest in signaling (here: degree of scent marking) to maintain dominance at a

particular life history stage. However, the lack of correlation between dominance and body mass observed here could be the result of ideal living conditions in the laboratory. Prior to experimentation, males were provided with food *ad libitum*. Body weights attained under such conditions may not reflect those attained in competitive situations in the field.

In bank voles, males of large body mass have larger testes than males of small body mass (Ylönen *et al.* 2004). Testis size is thought to be related to reproductive success in promiscuous species, because larger testes produce sperm at higher rates (Ginsberg & Huck 1989, Gomendio *et al.* 1998). In this study, however, we found no evidence for a relationship between male body mass and reproductive success.

According to our results, sexual selection for male dominance or male body mass may not be strong in bank voles. However, the intensity of sexual selection depends on the operational sex ratio, the number of receptive females to fertile males (Emlen & Oring 1977). If the operational sex ratio is female biased, male-male competition is expected to be reduced and sexual selection to be less intense. Although the sex ratio in the present experiment was female biased (2 males:4 females) the operational sex ratio was on average only 1.0. The reproductive success of dominant males, and males of large body size, was not influenced by the operational sex ratio, suggesting that the lack of a positive correlation of these traits and reproductive success was not caused by the experimental setup.

Why do female bank voles mate with multiple males irrespective of male dominance status or male size? A variety of benefits to females could explain multi-male mating (*see* Jennions & Petrie 2000 for review). Forced copulations — and tolerated copulations to reduce male harassment — can be excluded for bank voles since females initiate mating with multiple males (I. Klemme, S. Kataja-aho, J. A. Eccard & H. Ylönen unpubl. data). We therefore suggest two alternative explanations for multi-male mating in bank voles.

First, mating with multiple males might be a counterstrategy against male infanticide (*see* Wolff & Macdonald 2004 for review). Infanticide, committed by males, is common in bank

voles and may threaten female reproductive success (Ylönen *et al.* 1997). By mating with multiple males, females may confuse paternity, causing potential fathers to avoid killing their young. If so, females might be making “the best of a bad job” by choosing to mate additionally with males of poor quality (Wolff & Macdonald 2004).

Second, females may mate multiply to bet-hedge against genetic incompatibility and decrease the risk of reproductive failure by biasing paternity towards the most compatible male (Zeh & Zeh 1996, 1997). Female choice for good genes and post-copulatory female choice for compatibility can interact paradoxically (Colegrave *et al.* 2002). Colegrave *et al.* (2002) propose a model in which the selection pressure to either mode of female choice depends on the costs of incompatibility, the costs of multi-male mating, the costs of mating with low quality males, and the degree to which females are able to use post-copulatory mechanisms to bias paternity according to compatibility. The model shows that multiple mating is likely to be beneficial if the costs of incompatibility are high even if it involves mating with males of lower genetic quality. Since populations of bank voles undergo periodic density cycles (Krebs & Myers 1974) and therefore often pass through genetic bottlenecks, a high degree of inbreeding and concomitant genetic incompatibility is likely for this species. Moreover, the high variation in paternity outcome within enclosures observed in this study might be explained by genetic incompatibility, because compatibility depends upon the interaction between each separate female-male pair.

In conclusion, if male dominance plays a role in reproductive success we would have expected that the paternity of offspring would be strongly skewed in favor of the dominant male. However, we found similar proportions of offspring sired to any male involved in the experiment. We suggest that, in bank voles, the benefit of multi-male mating overrides that of mating with dominant males and consequently sexual selection for male dominance and body mass is not very strong. Despite these results, a clear social organization of males in natural and laboratory bank vole populations exists. Why did male dominance evolve in this species and what are its benefits if dominance does not increase reproductive suc-

cess? The fitness benefit to high ranking animals may become visible over the long-term. Males of high social status may, for example, have preferential access to food or less stressful social interactions with other individuals. As Dewsbury (1982) pointed out, such factors could prolong their reproductive life-span and enhance their lifetime reproductive success even though rank *per se* might not lead to a greater production of offspring in the short-term.

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