

The effect of male competition on female choice in Brandt's vole, *Lasiopodomys brandti*

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Received 15 August 2005; Accepted 21 June 2006

A b s t r a c t. The effect of male competition on female choice in the Brandt's vole (*Lasiopodomys brandti*) was studied in the laboratory. Using a two-way choice test, we showed that when males did not compete, estrous females preferred and mated with the dominant males, but non-estrous females preferred subordinate males. However, when males competed, all dominant males gained the priority to mate, and the amicable behaviour between males, regardless of their dominant status, and between non-estrous females increased, compared with the behaviour between males and the estrous females. These results showed that interactions among Brandt's voles were not only influenced by male competition but also by reproductive status of female voles.

Key words: Brandt's vole (*Lasiopodomys brandti*), society hierarchy, estrous status

Introduction

Social hierarchy is a main character and important part of social organization, for which it is regarded as the foundation for the maintenance of social system (P r e m n a t h et al. 1996, P i p e r 1997). Social status can determine mating opportunities and influence reproductive success in males (M i c h e n e r & M c l e a n 1996). A common view based on the theory of sexual selection is that dominant males can obtain more mating opportunities and leave more offspring than subordinate males (D e w s b u r y 1982). In rodents, when dominant males and subordinate males co-exist, the subordinate males leave less urine marks to gain the acceptance by the dominant male at the cost of decreasing attraction to females (R i c h & H u r s t 1998). Many studies have shown females prefer the odor of, and mating with, dominant males (C a r r et al. 1982, H o f f m e y e r 1982, W h i t e et al. 1984, D r i c k a m e r 1992, H o r n e & Y l ö n e n 1996). For example, dominant male cape ground squirrels (*Xerus inauris*) have more mates and have more mating opportunities than subordinate males (W a t e r m a n 1997, 1998). Female rat-like hamsters (*Cricetulus triton*) in estrus prefer the odor of dominant males (Z h a n g et al. 2001). In primates, females also select dominant males as their mates (W a l t e r s 1986). In some sex-reversed fishes, males prefer dominant females as their mating partners (B e r g l u n d & R o s e n q v i s t 2001). In contrast to this common view, Q v a r n s t r o m & F o r s g r e n (1998) argue that when the benefit of mating with dominant males is less than that of reproduction, females may select the subordinate males as mating partners.

The Brandt's vole *Lasiopodomys brandti* is considered a pest rodent in a typical steppe habitat. It is distributed mainly in the Baikal area in Russia, Mongolia, and Inner Mongolia

in China (S h i 1988, L i u et al. 1994). It usually breeds from late March to August. Its population density oscillates greatly between years. Outbreaks of voles occur once every 5–7 years. The mating system of the vole is still unclear (Z h a n g & Z h o n g 1981, F a n g & S u n 1991, X i e et al. 1994, W a n et al. 1998, Z h a n g & Z h a n g 2003). In nature, a family usually consists of one adult male, several adult females, and their offspring. The adult male may be the dominant individual in the family (W a n et al. 1998). Odor preference studies show that adult females investigate the odor of subordinate males more frequently than the odor of dominant males (Z h a n g & F a n g 1999).

Benefit-cost analysis shows that reproductively inactive females gain little from associating with dominant males. On the contrary, they may suffer injuries from aggressive behaviour of dominant males. In other words, male-female interactions should depend on both the dominant status of males and the reproductive conditions on females. Therefore, we hypothesize that estrous females prefer dominant males over subordinate males, whereas non-estrous females prefer subordinate males over dominant voles. To test this hypothesis, we used Brandt's voles to conducted two experiments by manipulating male dominance and female reproductive status to see how male and female interact based on these two factors.

Materials and Methods

All experimental voles were from the offspring of a wild population caught in Inner Mongolia in China in April to August in 2003. They were reared separately in plastic boxes (28.5 × 17.2 × 15.8 cm) in the laboratory and were provided with food and water *ad libitum*. The photoperiod was set at 16L: 8D, and the light period began at 05:00. Dim red light shone at all times. The temperature was set at 25 ± 1°C. Only mature and healthy individuals were selected for the experiment based on the degree of testis descendance for males or the open condition of the vagina for females. The individuals selected for our experiments were from different lineages and thus, they were not inbreeding lines. The mean body size was 39.73 ± 1.06 (SD) g of male ($n = 48$) and 31.74 ± 5.35 (SD) g of female ($n = 42$), respectively.

We determined social status of male voles by paired contest between two like-sized (less than 3 g difference in weight) males: the winner was the dominant male and the loser, the subordinate male. The estrous status of female was judged by the open condition of vagina as mentioned in Z h a n g et al. (2004), and only two statuses were classified, which were estrous and non-estrous status. We used a plastic box (90 × 30 × 30 cm) as the arena, which was divided into three equal compartments by two plastic planks, each of them with a hole (diameter: 15 cm) in the bottom.

To test how male competition influence male-female interaction, we set up two social conditions in our experiments: with (Experiment I) and without (Experiment II) male competition. In Experiment I, we put dominant male and subordinate male in the two side-compartments by using two tethers to confine their movement within their respective side-compartments. Thus male could not have physical contact between them. In Experiment II, males were not tethered and could move freely in the three compartments. In both experiments, we put a female in the central compartment. Before releasing it, we allowed it to adapt to the environment for fifteen minutes without social interaction. Then, we observed male-female interaction for ten minutes, either with (Experiment I) or without (Experiment II) body contact between the males. We identified individuals by cutting out unique patterns on the fur. After the completion of each observation period, the box was first rinsed using tap water and

then wiped clean with alcohol to remove residual odors. To minimize human interference, observations were recorded through a kinescope monitor.

We collected frequency data for the following behavioural patterns: sniffing, aggression, leaping, self-grooming, amicable behaviour, and mating (the definitions of these behavioural patterns follow Eklund (1996)). The normality of data distribution was tested by one-sample Kolmogorov-Smirnov method. Independent samples t test (when data distribution was normal) or Mann-Whitney test (when the normality prerequisite was violated) was used for testing the significance in the difference between the two treatment groups in either experiment. Wilcoxon paired-sample signed ranks test was used when comparing with paired data from the two groups. Pearson correlation coefficient was used for analyzing the association between different behavioural patterns. Chi-square test was used to test mate preference. The level of significance for all tests was set at $\alpha = 0.05$.

Results

Female choice in Experiment I

We found that aggression happened more frequently between dominant males and females than between subordinate males and females, regardless of female estrous status (see Tables 1 and 2). No significance was found in any other behavioural patterns.

In 12 choice tests, estrous females preferred to first associate with and mate with dominant males over the subordinate by 9 to 3 ($\chi^2 = 10.782$, $df = 1$, $P = 0.001$). Non-estrous females preferred dominant males (4 out of 12 times), but estrous females preferred

Table 1. Behaviour of estrous female in non-male competition experiment.

	Dominant male	Subordinate male	Wilcoxon Signed Ranks Test
F-S-M	6.17 ± 3.33 (12)	4.75 ± 2.90 (12)	Z = 1.298, P = 0.194
M-A-F	4.58 ± 3.94 (12)	1.08 ± 1.38 (12)	Z = 2.367, P = 0.018*
M-Am-F	1.83 ± 2.04 (12)	2.92 ± 2.81 (12)	Z = 1.272, P = 1.123
F-G	10.33 ± 10.54 (12)	4.83 ± 3.13 (12)	Z = 1.123, P = 0.262
MF	1.92 ± 2.15 (12)	1.00 ± 0.95 (12)	Z = 0.992, P = 0.322
P	4.58 ± 3.63 (12)	5.08 ± 4.30 (12)	Z = 0.582, P = 0.560

Note: F-S-M: sniffing between male and female; M-A-F: agnostic behaviour between male and female; M-Am-F: amicable behaviour between male and female; F-G: self-grooming of female; MF: mating frequency; P: preference frequency; *: $p < 0.05$.

Table 2. Behaviour of non-estrous female in non-male competition experiment.

	Dominant male	Subordinate male	Wilcoxon Signed Ranks Test
F-S-M	4.08 ± 3.09 (12)	4.92 ± 4.34 (12)	Z = 0.534, P = 0.593
M-A-F	2.00 ± 2.66 (12)	0.50 ± 1.24 (12)	Z = 2.047, P = 0.041*
M-Am-F	3.25 ± 2.99 (12)	4.33 ± 3.39 (12)	Z = 0.833, P = 0.405
F-G	0.83 ± 1.70 (12)	0.83 ± 1.47 (12)	Z = 0.000, P = 1.000
P	7.42 ± 5.42 (12)	7.33 ± 5.53 (12)	Z = 0.628, P = 0.530

Note: F-S-M: sniffing between male and female; M-A-F: agnostic behaviour between male and female; M-Am-F: amicable behaviour between male and female; F-G: self-grooming of female; P: preference frequency; *: $p < 0.05$.

subordinate males (8 out of 12 times) ($\chi^2 = 25.00$ $df = 1$ $P = 0.003^* < 0.05$). No mating happened between male and female voles.

Female choice in Experiment II

Estrous females mated with dominant males more often than with subordinate males (see Table 3). No other difference was found.

Non-estrous females sniffed and amicably interacted more frequently with dominant males than with subordinate males (see Table 4).

Table 3. Behaviour of estrous female in male-competition experiment.

	Dominant male	Subordinate male	Wilcoxon Signed Ranks Test
F-S-M	2.58 ± 1.93 (12)	2.42 ± 1.93 (12)	Z = 0.720, P = 0.472
M-A-F	4.42 ± 3.32 (12)	2.42 ± 2.64 (12)	Z = 1.573, P = 0.116
M-Am-F	1.17 ± 1.70 (12)	1.25 ± 2.34 (12)	Z = 0.184, P = 0.854
MF	2.08 ± 1.88 (12)	0.33 ± 0.65 (12)	Z = 2.552, P = 0.011*

Note: F-S-M: sniffing between male and female; M-A-F: agnostic behaviour between male and female; M-Am-F: amicable behaviour between male and female; MF: mating frequency; *: $p < 0.05$.

Table 4. Behaviour of non-estrous female in male-competition experiment.

	Dominant male	Subordinate male	Wilcoxon Signed Ranks Test
F-S-M	4.08 ± 2.61 (12)	3.00 ± 1.65 (12)	Z = 2.066, P = 0.039*
M-A-F	3.67 ± 5.53 (12)	0.58 ± 1.24 (12)	Z = 2.530, P = 0.011*
M-Am-F	4.33 ± 2.81 (12)	3.67 ± 2.61 (12)	Z = 0.777, P = 0.437

Note: F-S-M: sniffing between male and female; M-A-F: agnostic behaviour between male and female; M-Am-F: amicable behaviour between male and female; *: $p < 0.05$.

Comparisons between Experiments I and II

For estrous females, sniffing frequency was higher in Experiment I than that in Experiment II for both dominant males ($t = 1.472$, $df = 22$, $p = 0.168$) and subordinate males ($t = 1.825$, $df = 22$, $p = 0.082$). Also shown was lower level of aggression and higher level of amicable behaviour in Experiment I than Experiment II with both dominant males ($t = 1.969$, $df = 22$, $p = 0.062$; $t = 2.100$, $df = 22$, $p = 0.047^*$) and subordinate males ($t = 2.272$, $df = 22$, $p = 0.033^*$; $t = 2.591$, $df = 22$, $p = 0.017^*$).

For non-estrous females, still male-female sniffing happened more often in Experiment I than that in Experiment II for both dominant males ($t = 1.707$, $df = 22$, $p = 0.102$) and subordinate males ($t = 1.818$, $df = 22$, $p = 0.083$). However, unlike the estrous females, aggression happened more often and amicable behaviour less often in Experiment I than those in Experiment II for both dominant males ($t = 0.467$, $df = 22$, $p = 0.645$; $t = 2.497$, $df = 22$, $p = 0.021^*$) and subordinate males ($t = 0.934$, $df = 22$, $p = 0.360$; $t = 0.678$, $df = 22$, $p = 0.505$).

Discussion

Male dominance may influence male's mating opportunity, which in turn influences their reproduction success (Michener & Mclean 1996). Active female choice may be

particularly difficult to demonstrate in natural situations where animals interact freely (Horne & Ylönen 1996). So small rodents have been the subject in a number of laboratory studies, and females have been shown to choose males actively according to their social rank (Carr et al. 1982, Drickamer 1992). Social rank can be founded through direct combat or indirect contact, for example, through scent marking as showed in many rodents and other animals. When dominant and subordinate males coexist, the quality of scent and marking frequency of subordinate males will lessen, though this can increase the toleration of dominant males to subordinates, the sexual attraction of subordinate males will also lessen (Rich & Hurst 1998). Females may prefer the odor of dominant males and mate with them; for example, the estrus female rat-like hamsters prefer the odor of dominant males (Zhang et al. 2001). But still some studies showed scent marking is only a side effect of male physiology, and females do not choose males by frequency of scent marking (Thomas 2002, Mech et al. 2003). Ferkin et al. (2004) found the physiological status of females also influences the mating choice.

Female preference can be affected by mating system (Shapiro & Dewsbury 1986). For example, female prairie voles (*Microtus ochrogaster*) prefer dominant males, but female mountain voles (*M. montanus*) have no such preference. The reason is that the mating system of the former is monogamous, whereas that of the later is promiscuous. Results of previous studies on mating system of Brandt's vole are disputed owing to the different methods used in the studies. For example, Zhang & Zhang (1981) studied the social structure of Brandt's vole. They showed the sex ratio in adults was female-biased. So they speculated that the mating system of Brandt's vole might be polygyny, or might even be promiscuity, but not monogamy. Fang & Sun (1991) believed that the mating system could only be social promiscuity, based on their study of the change of space structure in the Brandt's vole. Based on the reproductive results under different sex ratios in the laboratory, Xie et al. (1994) found that females could only breed in the presence of one male, not multiple males, and as such, they suggested that the mating system of Brandt's vole was probably polygyny and possibly monogamy. Wan et al. (1998) found that Brandt's vole had a family group in which one mature male lived with several mature females and their offspring during the breeding season in the field. So they believed that the mating system the Brandt's vole was polygyny. Zhang & Zhang (2003) regard it is prone to monogamy and polygyny based on the influence of operational sex ratio on mating behaviour in the Brandt's vole. So up to now, we still cannot give a solid conclusions on this questions. In our study, if the relationship between mate preference and mating system also holds in the Brandt's vole, its mating system should be close to monogamous as our study shows that females preferred mating with the dominant males, despite the fact that no mate preference exhibited in the experiment without male-male competition (Experiment I). It seems that an integrative approach including molecular biology, genomics, neuroscience, behavioural biology and evolutionary biology is needed to clarify this issue, as Robinson et al. (2005) suggested.

Male competition and female choice can happen at three levels: choice in precopulatory stage, choice after postcopulation and before prefertilization, and choice in postfertilization stage (Eberhard 1996). If we put our experiment in perspective, male-male competition may be persistent in natural conditions. For example, Huck et al. (1986) have found that, immediately after mating, dominant male golden hamsters (*Mesocricetus auratus*) mount females less frequently than other males do with the same females (the Coolidge effect). This provides an opportunity for subordinate males to mate with the females. In primates,

mating between females and subordinate males is prone to be interrupted by dominant males (Wilson 1981, Manson 1996). Thus, subordinate males adopt the tactic of short-duration mating (Rood 1972). In our study, although we failed to find any significant difference in mating frequency between dominant and subordinate males in the experiment without male-male competition, the mating frequency of dominant males was much higher than that of subordinate males in the experiment where males competed. This result is consistent with our previous study that male Brandt's voles interfere with one another during mating (Zhang & Zhang 2003).

Compared with frequency of behaviour in the experiment without competition, the frequency of the same behaviour in the experiment with male-male competition tended to be lower. The reason may be due to mating interference among males in the latter, where aggression between males and estrous females increased while amicable behaviour decreased. This may be due to mate competition during mating. Unlike estrous females, non-estrous females interacted less aggressively with males. This may be because males can increase their mating opportunity via familiarizing themselves with females. So our results show that both male dominance and female reproductive status can profoundly influence the pattern of male competition and female choice.

Acknowledgements

This study was funded by a grant from the Chinese National Science Foundation (CNSF Project 30270881). Especially thanks to two referees for their precious suggestions and editorial board of *Folia Zoologica* for their patients on this manuscript.

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