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## BEHAVIOURAL REACTION OF ROOT VOLE (*MICROTUS OECONOMUS PALLAS*) MALES OF DIFFERENT SOCIAL RANKS TO FAMILIAR AND NOVEL ODOUR OF CONSPECIFIC MALES

**ABSTRACT:** In this experiment, we tested the hypothesis that males of root voles (*Microtus oeconomus* Pallas) of different social ranks display different behavioural strategies. To document behavioural differences between social ranks, we investigated patterns in the behavioural responses to urine cues from familiar and novel individuals in a choice maze. Ten pairs of male voles were effectively used in this experiment. All behaviour was recorded with OBSERVER 5.0. When experiment was finished, video tapes were transformed into digital data. Then all data were analyzed by SPSS. The results showed that the approach latency of subordinates was shorter for familiar odours than novel ones, dominant individuals preferentially entered the strange odourant box, subordinates preferred familiar odours over novel ones, subordinates spent more time visiting familiar odours compared to the novel odours, dominants preferred novel odours to familiar ones, subordinates approached familiar odours more frequently than novel ones and self-groomed more often in the familiar odourant box than in the novel box, and dominant and subordinate individuals showed significantly different countermarking behaviours to familiar and novel odours. In conclusion, the dominants and subordinates displayed different behaviour patterns when faced to familiar and novel conspecific males' urine cues. The data support our hypothesis that differences in social rank induce differences in behavioural patterns.

**KEY WORDS:** root vole (*Microtus oeconomus* Pallas), social rank, odour cue

### 1. INTRODUCTION

Odour cues from rodent urine, which play an important role in individual recognition, carry considerable social information regarding gender, status, and individuality (Hurst *et al.* 2001). Differences in urine quality between dominant and subordinate males can be detected by other males (Hurst 1990), resulting in different behavioural responses by conspecifics (Sun *et al.* 2006). By assessing their potential opponents through urine cues, individuals may be able to predict the probable outcome of social encounters and decide which strategy to adopt (Grafen 1987).

Competition and defence of territories can cause strong selection on any behaviours that animals use to defend habitats and mates. Although agonistic reaction to the introduction of an unfamiliar conspecific seems to be an important mechanism for successful protection from intruders (Desjardins *et al.* 1973), individual responses differ between social ranks. Dominant male mice, *Mus musculus* L., aggressively defend their home

territories against neighbors and unfamiliar intruders (Hurst 1987), while subordinates deposit only a few urine marks in response to novel odours in their environment (Hurst 1990). These responses suggest that dominant and subordinate males exhibit different behavioural responses to odours from neighboring (familiar) or novel males.

The root or tundra vole (*Microtus oeconomus* Pallas, 1776), being the only extant Holarctic member of the species-rich genus *Microtus*, is an interzonal small mammal that occurs in the wet grasslands of both the Arctic and temperate zones (Brunhoff *et al.* 2003). Field studies on root voles have primarily documented their home range, dispersal patterns, and population changes (Tast 1966, Sun *et al.* 1982, Gundersen and Andreassen 1998, Aars and Ims 2000), showing dimorphism in home range (males > females) and male-biased dispersal (see Table 1).

Recently, our laboratory studies regarding mate choice, social recognition, and parental care have suggested that root voles in the Qinghai-Tibet Plateau may be a polygynous species (Zhao 1997, Zhao *et al.* 2002, 2003, also see Table 1), a finding consistent with previous predictions (Heske and Ostfeld 1990). Females preferred dominant males to subordinate males, indicating a great disparity in competitive ability for mating between males of different social ranks (Zhao *et al.* 2003). However, little is known regarding the displays performed by male root voles of different social ranks. In this experiment, we tested the hypothesis that differences in

social rank result in different behaviour patterns among male root voles, i.e., dominants would show a preference for novel urine, whereas subordinates would prefer familiar odours.

## 2. MATERIAL AND METHODS

### 2.1. Study animals

Wild root voles were captured from a meadow in Menyuan County (37°29'–37°45'N, 101°12'–101°23'E), northwest of Xining City in Qinghai Province, China. Laboratory colonies were established at the Northwest Plateau Institute of Biology in Xining City.

The male root voles used in this study (subjects and objects) were F3 generation offspring from field-captured animals, and were reared under a long-day photoperiod (14:10 h light:dark cycle, lights on at 0800 Beijing Standard Time). Animals were maintained in clear polycarbonate cages (40 × 28 × 15 cm), which contained wood chip bedding and cotton nesting material. Room temperature was maintained at 22 ± 2 °C. Food (BLARC, China) and water were provided *ad libitum*. Once a week, cages were cleaned and cotton-nesting material was replaced. All male animals used in the experiment were 90–120 days old and weighed between 24 and 35 g. Sibling pairs were raised together from birth until their experimental trial. Female siblings were reared apart after weaning at day 20. None of the experimental animals had experienced copulation.

Table 1. Characteristics of the root vole (*Microtus oeconomus*).

	Characteristics	References
Dimorphism in home range	Male > Female; A male will overlap with several females	Tast 1966, Sun <i>et al.</i> 1982
Dimorphism in body weight	Male > Female	Zhao 1997, Zhao <i>et al.</i> 2003
Sex-biased dispersal	Male: yes; Female: no	Tast 1966, Sun <i>et al.</i> 1982, Gundersen and Andreassen 1998, Aars and Ims 2000
Dimorphism in mate choice	Female: prefers familiar males to novel ones; Male: no choice	Zhao 1997, Zhao <i>et al.</i> 2002, 2003
Dimorphism in parental care	Female > Male	Zhao 1997

## 2.2. Experimental equipment

The behavioural choice maze included two odourant boxes ( $30 \times 30 \times 30$  cm) and one neutral box ( $30 \times 30 \times 45$  cm); the boxes were constructed from organic glass (Fig. 1). The odourant boxes were connected to the neutral box by pellucidly organic glass tubes ( $20$  cm long,  $7$  cm diameter). A culture dish containing fresh urine was put in the centre of each odourant box, providing a stimulant. A switch controlled the passage of experimental voles between the odourant and neutral boxes.

## 2.3. Experimental procedure

### 2.3.1. Dyadic interaction test

The social rank test was conducted by means of dyadic interactions 5 days before the behavioural test. Twelve pairs of healthy male sibling voles were employed in this test; each pair was used only once. Sibling pairs were reared together after weaning at day 20. One sibling in each pair was larger (by body weight) than the other ( $32.2 \pm 0.9$  vs.  $25.1 \pm 1.2$ ,  $P < 0.01$ ). Little aggressive behaviour resulting in injury occurred between the adult siblings during dyadic interactions; the distinct differences in body size during this test simplified the determination of social rank (Zhao *et al.* 2003).

Clear polycarbonate cages were divided into two compartments using wire grids and jealous-glass, which is a thick, ribbed, and nontransparent glass. At the bottom, a layer of sopping-water paper was spread. Two males were placed in the box, one in each compartment. The jealous-glass was removed 2 min after the placement of the males, and the trials ran for 4 min. If neither urine nor feces marks were observed within the 4-min period, the test was considered ineffective. Urine odour can provide information regarding the signaller's social rank (Drickamer 2001); thus urine marks on the sopping-water paper, as well as the quantity of feces deposited, was recorded for each individual male vole and used as the criteria for social rank estimation.

### 2.3.2. Odour habituation for familiar relationship

Additional pairs of healthy males, 10 pairs in total, were used as stimuli that corresponded to the body weight/age pattern of the sibling pairs, but were not related to the experimental animals. Each pair was used only once. Wood chip bedding containing urine was removed from the home cage of one of the two stimulus animals (the individual was selected randomly) and placed in a clean cage. Twice each day (09:00 and 15:00) during a 4-day period (eight exposures in to-

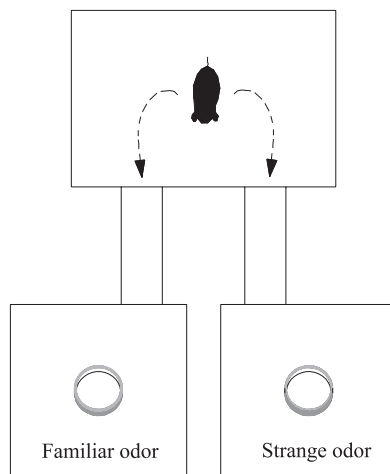


Fig. 1. The experimental apparatus used to test behaviour choice. The odourant boxes ( $30 \times 30 \times 30$  cm, bottom) and neutral box ( $30 \times 30 \times 45$  cm, upper) were made of organic glass. The odourant boxes and the neutral box were connected by pellucidly organic glass tubes ( $20 \times 7$  cm). The culture dishes containing fresh urine from either a familiar or a novel vole were put in the centre of the odourant boxes as a stimulant. A switch controlled the movement of voles between the odourant and neutral boxes.

tal), a male subject was placed in the cage and allowed to habituate to the stimulus for 1 h. After the 4 habituation days were completed, the individual was used in the odour choice test. During the odour choice test, the odour donor was considered a familiar stimulus to the subject and a second individual was regarded as a novel stimulus.

Male root voles may have encountered some of the other males in the field, but the novel signallers had no genetic relationship with the subjects, and the subjects and novel odour donors in this experiment were kept in isolation before the test. Therefore, the effects of any previous contests and kinship could be excluded.

### 2.3.3. Odourant preparation

On the day of the odour choice test, the stimulus male voles were taken out of their home cage and placed on the covers of the clear cages. Two layers of gauze were used to separate feces and urine. A piece of absorbent cotton was used to collect fresh urine from either a familiar or novel donor and was placed in a culture dish as the odourant. To ensure that only fresh odours were encountered during the trials, urine more than 20-min-old was not used.

### 2.3.4. Behavioural record during odour choice tests

The behavioural tests, including the odour habituation tests, were conducted in a separate room in which the temperature, lighting, and aeration conditions were identical to the breeding room. The tests lasted 10 min and were conducted during the light phase, between 09:00 and 18:00. Initially, the experimental animal was placed in the neutral box; the tubes were then opened, allowing the individual to freely enter either of the two choice boxes during a 5-min period. The animal was then returned to and confined within the neutral box, and two dishes, each containing urine from a different donor, were placed in the centre of the two odourant boxes (one dish to each box) at the same time. Two minutes

later, the tubes were opened again and the behavioural test began. If the subject male remained within the neutral box for 5 min and/or stayed in the tube without entering either of the odourant boxes for more than 3 min, the trial was terminated and excluded from statistical analysis.

During the 10-min trials, the following behavioural variables were recorded with OBSERVER 5.0: approach latency (the time spent by the animal before entering either of odourant boxes and approaching one of the odourant dishes for the first time), visit duration (the time an individual remained in either of the two odourant boxes after entering it), and the time spent sniffing the odourants (the individual brought their nostrils to within 0.5 cm of the odourant dish and obviously sniffed the contents). Meanwhile, the number of approaches (the individual came within approximately 1 cm of the stimulus without evidently sniffing it), self-grooming events, and countermarks (urine strips, urine speckles, feces around the odourant dishes; these are evidence of either over-marking or adjacent-marking (Ferkin 1999) were recorded for each trial. A 30-min interval elapsed before the next consecutive test commenced. The apparatus was cleaned with a 75% alcohol solution, washed with clear water, and dried with an electric dryer between trials.

### 2.3.5. Statistical analysis

When experiment was finished, all video tapes were transformed into digital data. The behavioural variables were treated as an index of time (seconds) or frequency. The statistical analyses were performed using SPSS11.0 (treatment as mean  $\pm$  SE. To estimate their social rank, the differences in urine and feces marks between two male siblings in the dyadic interactions were analysed using Wilcoxon's test, and the differences in the subjects' behavioural responses to either familiar or strange odours were also compared with this test. The differences in the behavioural response patterns between dominant and subordinate individuals to strange odours was analysed using Mann-Whitney tests. The differences were regarded as statistically significant at  $P < 0.05$ .

### 3. RESULTS

#### 3.1. Determination of social ranking between two male siblings by urine marking

The number of urine and feces markings made by two male root voles during a dyadic interaction was analysed by Wilcoxon's test (Table 2). The results indicated significant differences in the number of urine and feces marks between two male voles during dyadic interaction, and therefore, the number of urine and feces marks can indicate social ranking (Table 2).

#### 3.2. Response of males in different social ranks to urine odours from different male donors

The results showed that subordinates entered the familiar odourant box significantly earlier than the strange odourant box (Fig. 2A;  $P = 0.037$ ), whereas dominant individuals approached the strange odourant box considerably earlier than the familiar one (Fig. 2A;  $P = 0.011$ ). Comparing visit duration, subordinates spent less time visit-

ing the novel odour box than the familiar one (Fig. 2B;  $P = 0.037$ ), while dominant individuals spent more time visiting the novel odour box than the familiar one (Fig. 2B;  $P = 0.011$ ). No significant difference was found in the time subordinates spent sniffing either the familiar or strange plates (Fig. 2C;  $P = 0.241$ ), but dominant males spent much more time sniffing the novel odourant plate than the familiar one (Fig. 2C;  $P = 0.008$ ).

Differences in the frequency of approaching, self-grooming, and countermarking by either dominant or subordinate individuals were analyzed using Wilcoxon's test. When given a choice between the familiar odour box and the strange one, subordinates approached the familiar odour more frequently than the strange one (Table 3;  $P = 0.032$ ), while dominant males showed no bias for either the familiar or the strange odours (Table 3;  $P = 0.088$ ). Subordinates self-groomed significantly more in the familiar odourant box than in the strange one (Table 3;  $P = 0.035$ ). Conversely, dominant males self-groomed significantly more in the strange odourant box than in the familiar one (Table 3;  $P = 0.030$ ). In addition, subordinates showed no bias between exploring the odours from

Table 2. Urine marks (mean  $\pm$  SE) of dyadic interaction of male siblings in root vole (*Microtus oeconomus*). Numbers in parentheses indicate sample sizes.

	Male with larger body size as the dominant	Male with smaller body size as the subordinate	Wilcoxon's test
Urine marks	4.10 $\pm$ 0.43 (10)	2.70 $\pm$ 0.30 (10)	$P < 0.01$
Feces marks	5.90 $\pm$ 0.28 (10)	4.60 $\pm$ 0.22 (10)	$P < 0.05$

Table 3. Behavioural response in frequencies (mean  $\pm$  SE) of male subordinates and dominants to male familiar and strange odours in root voles (*Microtus oeconomus*)

Behavioural Index	Subordinate males ( $n = 10$ )			Dominant males ( $n = 10$ )		
	Familiar odour	Strange odour	Wilcoxon's test	Familiar odour	Strange odour	Wilcoxon's test
Approach (no./10 min)	4.70 $\pm$ 0.82	2.40 $\pm$ 0.69	$P = 0.032$	1.33 $\pm$ 0.69	3.22 $\pm$ 0.92	$P = 0.088$
Self-grooming (no./10 min)	12.70 $\pm$ 2.70	3.40 $\pm$ 1.21	$P = 0.035$	2.56 $\pm$ 1.52	13.22 $\pm$ 4.14	$P = 0.030$
Countermark (no./10 min)	1.40 $\pm$ 1.11	1.30 $\pm$ 1.10	$P = 1.000$	0.22 $\pm$ 0.22	2.00 $\pm$ 0.88	$P = 0.042$

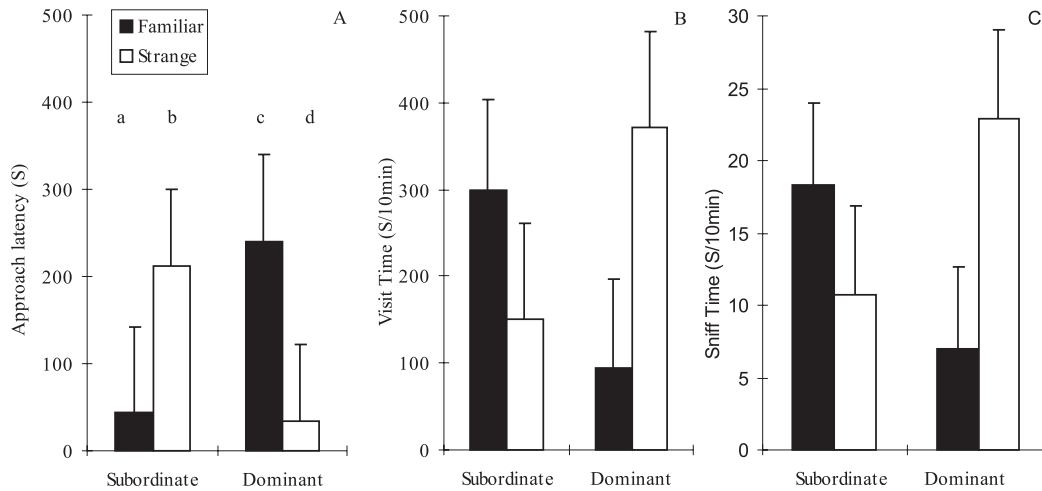


Fig. 2. The responses of subordinate and dominant male root voles (*Microtus oeconomus*) to odours from the urine of familiar and strange males ( $n = 10$ ). The behaviours examined were A: approach latency, B: visit time, and C: sniff time. The  $a$ - $b$  (Wilcoxon's test) indicated significant differences for behaviours A and B (both  $P < 0.05$ ), but not for behaviour C ( $P > 0.05$ ), while the  $c$ - $d$  (Wilcoxon's test) showed significant differences for behaviours A, B (both  $P < 0.05$ ), and C ( $P < 0.01$ ). The  $a$ - $c$  (Mann-Whitney test) showed significant differences for behaviours A ( $P < 0.01$ ), B ( $P < 0.001$ ), and C ( $P < 0.05$ ). The  $b$ - $d$  (Mann-Whitney test) indicated significant differences for behaviours A ( $P < 0.05$ ) and B ( $P < 0.001$ ), but not behaviour C ( $P > 0.05$ ).

the familiar or the strange individual and countermarked with equal frequency in either box (Table 3;  $P = 1.000$ ). Dominant individuals produced very few countermarks in response to the familiar odour, although they countermarked more frequently in response to the odours from the strange individuals (Table 3;  $P = 0.042$ ).

The responses of dominant individuals and subordinates to odours from strange males were analyzed using a Mann-Whitney  $U$ -test. The results indicated significant differences between the dominant individuals and the subordinates in their approach latency (Fig. 2A;  $P = 0.018$ ) and visiting time (Fig. 2B;  $P = 0.000$ ), but not in sniffing time (Fig. 2C;  $P = 0.067$ ).

#### 4. DISCUSSION

Our results from the dyadic interaction experiment confirmed that the urine of male root voles can be used by conspecifics to assess the social rank of the signaler (Drickamer 2001). Additionally, our hypothesis that male root voles of different social rank exhibit different behavioural strategies was

validated by our observations. Our laboratory results showed that dominant males displayed greater preference for exploring urine cues from novel males, whereas subordinates showed a greater affinity for cues from familiar males (Fig. 2; Table 3).

Within social systems, access to limited resources such as mates and territories often generates a conflict between same-sex conspecifics, increasing the possibility of agonistic interactions (Zhao 1997). Escalation of aggressive behaviours may result in serious injuries (Gosling *et al.* 1996), which may drastically reduce fitness. In this context, evolutionary theory suggests that animals should adopt strategies to avoid or minimize their level of aggressive interactions, thereby reducing the associated costs (Smith and Parker 1976, Gosling *et al.* 1996). By assessing their potential opponents, individuals may be able to predict the probable outcome of social encounters and finally decide whether to initiate aggression. Our data suggest that individuals of different social rank adopt different behavioural strategies (Fig. 2; Table 3), i.e., subordinates spent more time in their own territory, dis-

playing little bias toward their neighbours (Table 3), approaching familiar scents more preferentially (Fig. 2) and frequently (Table 3) than strange odours. Our data suggest that dominant males exhibit greater bias to their neighbors' odours (Fig. 2), while subordinate individuals show greater preference to familiar odours (Fig. 2).

Self-grooming is a motor behaviour directed to the outer body surface of an animal. In a social context, self-grooming broadcasts information to conspecifics (see review in Spruijt *et al.* 1992). In our experiment, we found that subordinates self-groomed significantly more in the familiar odourant box than in the strange odourant box and that dominant males self-groomed significantly more in the strange odourant box than in the box containing the familiar odour (Table 3). Therefore, our results suggest that the identity of individuals in terms of social rank may influence the self-grooming rates between individuals.

Many previous studies have suggested that dominant male mice advertise their identity and dominance to conspecific males by depositing urine marks on all surfaces within their territory (Hurst 1990) and by countermarking, which is more appropriate as a generic term for both over-marking and adjacent-marking (Ferkin 1999, Johnston 2003), those deposited by their competitors (Drickamer 2001). This pattern of marking provides a cheat-proof signal since only males that are able to dominate an area successfully can ensure that their own marks are predominate there (Gosling 1982). In contrast, subordinate mice reduce their urine marking behaviours dramatically after repeated defeats in agonistic interactions (Desjardins *et al.* 1973) and deposit only a small number of urine marks in response to newcomers in their environment (Hurst 1990). We found that subordinates counter-marked equally frequency in the two boxes, while dominant males countermarked more frequently in response to a novel odour than to a familiar one (Table 3).

Several developments from many cross-disciplinary studies involving fields such as neurobiology, anatomy, physiology, and chemical and molecular biology, have profoundly affected our understanding of odou-

rants and the receptor systems that are essential for social recognition and behaviours for many mammal species. For example, odourant molecules from the urine of sharp-nosed mammals such as rodents and canines can be detected by conspecifics through their vomeronasal organ (VNO) in the nose (Keverne 1999). It has been extremely difficult to define the molecular nature of these odourants until recently, but the chemosignals perceived by VNO sensory neurons, called pheromones, can arouse instinctive behaviours because they relay information regarding gender, sexual and social ranks, dominance hierarchies, and individuality (Brennan and Keverne 2004). Considering these findings at microstructural levels, it is easy to understand our results regarding male recognition of novel odour from same-sex individuals. We believe that in the odourant boxes during our trials, the behavioural responses of male root voles to the stimuli derived from other males' urine revealed an individual's strategy regarding territorial defence.

In conclusion, our data suggest that the number of urine marks made during dyadic interactions can indicate the signaller's social rank. Differences in social rank result in different behavioural patterns. In other words, dominant individuals investigated novel odours more frequently, whereas subordinates preferred familiar urine. The determinants that decide the social rank of an individual animal within the group are not yet clear. The factors determining individual ranking may include genetics or the social conditions during an individual's development, among other possibilities. This research on the differences in behavioural strategy exhibited by male root voles of different social ranks will help to further understand processes regarding kin discrimination and mate choice.

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