

FAMILIARITY AND MATE CHOICES OF FEMALE AND MALE ROOT VOLES (*MICROTUS OECONOMUS*) IN FEMALE NATURAL ESTRUS *

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Abstract : Many behavioral experiments compared monogamous species with polygamous one in microtine rodents show that the mating systems are associated with mate choice among individuals, and a major component determining nature of the sexual selection is familiarity between males and females. The long- and short-term effects of familiarity on both sexes' mate choices of root voles (*Microtus oeconomus*) was examined by three kinds of laboratory experiments. They were mate preference of the experimental root voles for the familiar versus the unfamiliar, the partner versus the unfamiliar and the partner versus the familiar stimulus ones. Familiarity was established by housing a male with an unrelated female in a plastic breeding cage for 8 h each day until they were found to display sexual behaviors. Partnership referred as the relationship between a pair of male and female having bred at least one litter of offspring. During a 30 min trial, two stimulus voles were tethered in two choice chambers of a Y-shaped maze respectively, while the experimental vole was allowed to enter either of the two choice chambers from the central arena. The experimental vole was scored for duration and frequency of visit, social-investigation, copulatory behavior, aggression and amiability with each stimulus vole. Behavioral comparison between the two stimulus voles was achieved by a Wilcoxon matched-pairs test. The results showed that the females preferred the familiar rather than unfamiliar males, the partner rather than unfamiliar males, the partner rather than familiar males in the social behaviors except for copulatory behavior with no significant level. However, the males made no a preference for the familiar versus the novel females, nor the partner versus the novel females. These data suggested that female preference for familiar males and males having no mate choice between familiar and strange females may be proximate behavioral processes underlying traits in mating system of root voles. Thus, female mating monogamously and male non-monogamously can be explained by the hypothesis that the mating system could be polygynous in root voles.

Key words : Root vole (*Microtus oeconomus*); Mate choice; Familiarity; Mating system

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Since the classic paper on mating system was firstly issued by Emlen and Oring^[1], many documents have shown that the mating system is the outcome of social behavioral interactions among intraspecific individuals which results in maximum reproductive effort^[2]. In rodents, species of microtine are elegant animals examined the relationship between mate choice and mating system.

Many experiments compared among different microtine species have proved that mate choices among individuals are associated with mating system of population^[3~7]. To establish relationship between mating systems and individual behaviors concerns many factors of which familiarity is an important one^[8~11]. For example, female and male both preferred the familiar opposite sex to the unfamiliar in mate choice in monogamous prairie voles (*Microtus ochrogaster*), did female and male both not so in non-monogamous montane voles (*M. montanus*)^[8]. And It has been proved that effect of familiarity on social interactions in voles is of long-term and short-term^[9,12].

Many previous studies focused on comparison between monogamy and polygamy vole species, i. e., the prairie vole and montane vole^[8,13~16], the prairie vole, pine vole (*M. pinetorum*) and meadow vole (*M. pennsylvanicus*)^[5,17~20]. As it is known now, the prairie vole, and pine vole is clarified as monogamous vole species, while the montane vole and meadow vole as promiscuous ones^[21,22]. Polygamous species are the vast majority of microtine, and can be divided into two categories: polygyny and promiscuity. However, study on direct comparison in mate choice between polygynous and promiscuous vole species has not been reported yet. The reproductive strategy and fitness are different greatly between polygyny and promiscuity, so the comparison in mate choices between the polygynous and promiscuous vole species is significant and necessary.

The mating system of root vole (*Microtus oeconomus*) population in Qinghai-Tibet Plateau might be polygamy based on the home range study^[23]. The populations in tundra in west of Canada was polygynous derived from field data^[24]. Thus, the goal of present study was to investigate the mating system of root voles from the perspective of behavioral experiments. The effects of familiarity on mate choice of root voles were analyzed by three kinds of laboratory tests of experimental animals' preferences for the familiar vs. unfamiliar, the partner vs. unfamiliar, and the partner vs. familiar stimulus animals.

1 MATERIAL AND METHODS

Root voles were captured in the site of Haibei Alpine Meadow Ecosystem Research Station of Chinese Academy of Sciences which is located northwest of Qinghai-Tibet Plateau with (37°29' ~ 37°45' N, 101°12' ~ 101°23' E). The animals were from the F1/F3 generation of breeding colonies, 3 ~ 6 months of age, individually housed in clear plastic cages (29 cm × 19 cm × 13 cm) with free access to Purina rabbit chow, carrot and water. The animals were

maintained in a 14/10 h light/dark photoperiod with light on at 1900 h and in 22~24 temperature.

The Y-shaped maze was used in this study for behavioral observation^[12,25]. It consisted of one neutral box (45 cm ×30 cm ×30 cm) and two choice chambers (30 cm ×30 cm ×30 cm). The choice chambers were attached with runway tubers (25 cm length and 7 cm diameter) connecting them to the neutral chamber. Two stimulus voles were tethered in the two choice chambers respectively so that they were not able to visit other chambers, while the experimental vole released from the neutral chamber was free either of the two choice chambers through the runway tubers.

Male and female siblings were housed separately after weaning. The sexual maturity was detected by scrotal or abdominal testis in males, and genital opening, closure of pubic symphysis and size of teats in females^[26,27]. All experimental animals were sexually experienced and females were made access to estrus naturally without artificial injection of estradiol benzoate and progesterone.

The experimental and stimulus voles were introduced into Y-shaped maze for 1 h day for 2 consecutive days prior to the behavioral test. On the test day, the experimental vole was placed in the neutral chamber and the two objects were tethered in the two choice chambers respectively for 10 minutes. Following this acclimation interval, the experimental vole was allowed to move freely in the maze. The behavior of experimental vole was recorded during 30 min test trial. Behavioral comparison between two stimulus animals was achieved by a Wilcoxon matched-pairs test.

An experimental vole was scored for the number and duration (in seconds) of visit to either of two tethered stimulus voles. In addition, duration and number of social behavioral patterns were recorded including of investigation (approach and sniffing / licking within 1 cm of the object's face, body, or anogenital region with the subject's snout), coquetry (allowance of a male object sniffing / licking her own genital region, or posture with her hip in facade of the male to induce him mounting by a female subject), courtship (a male subject displaying a circle-approach posture with estrous-cry and try to sniff / lick and mount a female object), copulation, aggression (attack or/and flight) and amiability (lying side/over, mutual grooming, grooming). Copulatory behavior in voles consists of three primary events: mount (of similar topography to a mount involved in a actual sexual behavior without vaginal penetration), intromissions (mount with insertion and intravaginal thrusting) and ejaculation (mounts with insertion and sperm transfer), which occur in organized series with each series terminated by an ejaculation^[8,15]. According to our observation to root voles, we regarded three primary events of copulatory behavior as two states: mount (without intromission by male, or female making similar act to male's mount) or mount by (female being mounted by male), lordosis/copulation (female keeping the "lordosis" posture accepting male's mount with intromission, ejaculation). Any test in which there was no visit nor social behaviors in-

cluding of copulatory behavior within 15 min was eliminate from samples.

2 RESULTS

2.1 Experiment 1

The present experiment was conducted to investigate whether root voles displayed sociosexual preference for the familiar versus unfamiliar mates.

Twelve experimental females with 12 familiar and 12 unfamiliar stimulus males or 11 experimental males with 11 familiar and 11 unfamiliar stimulus females were used in the present experiment respectively. A male experimental vole and an unrelated female were housed together in a plastic breeding cage (46 cm ×31 cm ×20 cm) for 8 h (at 1900) each day to established familiarity. The housing was stopped as soon as they were found to display sexual behaviors. Then, the trial started.

Table 1 Choice of familiar and unfamiliar males by female root voles in experiment 1
(Mean ±SE duration per 30 min period, in seconds)

Behaviors	Familiar males	Unfamiliar males	Wilcoxn Test	Behaviors	Familiar males	Unfamiliar males	Wilcoxn Test
Visit	890.5 ±79.2	329.8 ±51.5	* *	Mount by	1.8 ±1.3	0.2 ±0.2	ns
Investigation	229.2 ±31.3	131.4 ±28.9	*	Lordosis	25.5 ±14.5	7.4 ±7.4	ns
Coquetry	11.5 ±6.1	0.5 ±0.5	*	Aggression	3.6 ±2.2	23.4 ±7.3	*
Mount	0.1 ±0.1	0.0 ±0.0	ns	Amiability	157.9 ±43.5	0.2 ±0.2	* *

* $P < 0.05$; * * $P < 0.001$; ns: no significance; Sample size: $n = 12$

Table 2 Choice of familiar and unfamiliar females by male root voles in experiment 1
(Mean ±SE duration per 30 min period, in seconds)

Behaviors	Familiar females	Unfamiliar females	Wilcoxn Test	Behaviors	Familiar females	Unfamiliar females	Wilcoxn Test
Visit	610.8 ±47.7	601.4 ±34.4	ns	Copulation	1.7 ±1.7	0.0 ±0.0	ns
Investigation	135.9 ±21.3	189.5 ±23.0	ns	Aggression	6.4 ±3.5	26.9 ±5.1	*
Courtship	37.9 ±12.1	71.6 ±20.2	*	Amiability	64.3 ±26.9	10.4 ±9.8	*
Mount	4.5 ±3.5	0.0 ±0.0	ns				

* $P < 0.05$; ns: no significance; Sample size: $n = 11$

Results of preference for the familiar versus unfamiliar males by female root voles are summarized in Table 1. Female root voles visited, socially investigated, coquetted and amiably interacted with the familiar males more than with the unfamiliar males and aggressed the familiar males lesser than the unfamiliar males significantly in duration. While male root voles did not display a significant preference for the familiar or unfamiliar females in duration of visit, investigation and copulatory behaviors (Table 2). Although they interacted by significantly more aggression with unfamiliar females than with familiar females, males courted significantly more time to unfamiliar females than to familiar females. Males showed signifi-

cantly more amiability to familiar females than to unfamiliar females, however, the duration of amiability spent with familiar females by males was less compared to that with familiar males by females (Table 1, Table 2). { These results suggested that males were short of a mate choice between the familiar and unfamiliar females}.

2.2 Experiment 2

In the present experiment, we aimed to investigate the behavioral preference for the partner versus unfamiliar males or females by female or male root voles, respectively. Twelve experimental females with 12 partner and 12 unfamiliar stimulus males or 11 experimental males with 11 partner and 11 unfamiliar stimulus females were involved in the present experiment, respectively. Partnership stood for the relationship between a male and a female having bred at least one litter prior to the test. The tests were conducted during 12 ~ 24 h after parturition.

Table 3 Choice of partner and unfamiliar males by female root voles in experiment 2
(Mean \pm SE duration per 30 min period, in seconds)

Behaviors	Partner males	Unfamiliar males	Wilcoxn Test	Behaviors	Partner males	Unfamiliar males	Wilcoxn Test
Visit	861.1 \pm 98.9	216.5 \pm 45.0	* *	Mount by	3.4 \pm 1.7	0.3 \pm 0.2	Cs
Investigation	212.0 \pm 51.0	75.6 \pm 12.8	* *	Lordosis	59.1 \pm 26.1	15.7 \pm 10.6	ns
Coquetry	25.1 \pm 12.7	1.0 \pm 0.7	* *	Aggression	19.5 \pm 12.0	13.6 \pm 3.1	ns
Mount	4.1 \pm 4.0	0.0 \pm 0.0	ns	Amiability	191.4 \pm 104.3	1.6 \pm 1.6	* *

* * $P < 0.01$; ns: no significance; Cs: close to significance; Sample size: $n = 12$

Table 4 Choice of partner and unfamiliar females by male root voles in experiment 2
(Mean \pm SE duration per 30 min period, in seconds)

Behaviors	Partner males	Unfamiliar males	Wilcoxn Test	Behaviors	Partner males	Unfamiliar males	Wilcoxn Test
Visit	562.5 \pm 114.8	620.7 \pm 107.7	ns	Copulation	4.6 \pm 4.6	27.3 \pm 16.2	ns
Investigation	119.5 \pm 28.8	177.6 \pm 28.4	ns	Aggression	13.8 \pm 5.7	21.8 \pm 5.6	ns
Courtship	23.3 \pm 13.8	49.5 \pm 24.2	ns	Amiability	83.6 \pm 33.2	21.0 \pm 19.2	ns
Mount	3.0 \pm 2.0	6.2 \pm 4.5	ns				

ns: no significance; Sample size: $n = 11$

Results of preference for partner or unfamiliar males by female root voles are given in Table 3. Females displayed a significant preference for the partner males in duration of visit, investigation, coquetry, and amiable interaction. They spent more time in receiving mount from the partner males than from the unfamiliar males with close to significance. They also spent more time in mount and lordosis to the partner males than to the unfamiliar males, but not significant. There was no a significant difference between the partner and unfamiliar males in duration of aggression interacted with each of them by females in the experiment, because the females' aggressive level to the partner males was creasing after parturition ac-

ording our observations. While males did not exhibit a significant preference for the partner versus unfamiliar females in duration of visit, investigation, courtship, copulatory behavior and aggression (Table 4).

2.3 Experiment 3

In the two above experiments, long- and short-term effects of familiarity on intersexual mate choices in root voles were examined. These results showed that familiarity affected only on the mate choice of the females. In the present experiment, we intended to test social-behavioral preference for the partner versus familiar males by female root voles so as to detect effect of familiarity on fidelity of female partners.

Fourteen experimental females with 14 partner and 14 unfamiliar stimulus males in this experiment. In the breeding cage of a pair of a female and a male which bred at least one litter before, a sexually experienced male was housed in a wire mesh box (20 cm × 6 cm × 6 cm) from the pair for 8 h each day aggregating 48 h until at the day of parturition. The male was familiarized with the pair one another and moved out to put alone in a new cage 2 h before test. The tests were conducted during 12 ~ 24 h after parturition.

Table 5 Choice of partner and familiar males by female root voles in experiment 3
(Mean ±SE duration per 30 min period, in seconds)

Behaviors	Partner males	Unfamiliar males	Wilcoxn Test	Behaviors	Partner males	Unfamiliar males	Wilcoxn Test
Visit	759.6 ±90.6	439.2 ±65.3	*	Mount by	0.3 ±0.3	0.0 ±0.0	ns
Investigation	161.7 ±29.6	185.1 ±27.8	ns	Lordosis	6.1 ±6.1	0.0 ±0.0	ns
Coquetry	8.4 ±4.3	2.6 ±1.4	ns	Aggression	3.4 ±1.2	23.4 ±5.5	**
Mount	0.2 ±0.2	0.0 ±0.0	ns	Amiability	256.3 ±78.1	27.0 ±17.0	**

* $P < 0.05$; ** $P < 0.01$; ns: no significance; Sample size: $n = 14$

The females visited their partner males significantly more, aggressed significantly less than the familiar males (Table 5). The females also spent significantly more time visiting and interacting amiably with, and less time aggressing to their partners than with the familiars.

3 DISCUSSION

3.1 Mate choice and mating system

In this study, female root voles did not significant preference of copulatory behaviors for the familiar or partner males versus the unfamiliar males without significance, but they preferred familiar males to unfamiliar males in other social behaviors (Table 1, 3). Moreover, Females preferred partner males to familiar males in the other social behaviors (Table 5). Without respect to copulatory behaviors for testing females access to natural estrus and the short test duration, females were exposed to have a mate preference for the familiar or part-

ner males in general. These data suggested female root voles tended to mate monogamously. On the other hand, male root voles had no mate choice both between familiar and unfamiliar, partner and familiar females (Table 2, 4), suggesting that males tend to mate polygynously.

Mate choice among intersexual individuals can be reflect the character of mating system of vole species and may be proximate behavioral process underlying traits in mating system^[5,7]. Our laboratory results, female mating monogamously and male polygynously can be explained by the hypothesis that the mating system of root voles is polygyny. Our findings were consistent with Lambin et al. who suggested that the root vole's mating system is polygyny according to the home range study in Canada's western Arctic^[24]. Spacing system of root voles is diversity resulting in flexibility of its mating system. In Europe populations of the root vole, Tast found that adult females were of territoriality with forming cluster and male were territorial^[28]. Ostfeld considered the root vole studied by Tast as a species with territorial females^[28,29], while Cockburn as a species with maternal cluster and territorial male^[30]. In 60s and 80s of this century, Russian and Polish studies on root voles found the two contrary results^[31]. In southern Norway populations of the root vole, several reproductive females share the same home range^[32]. Gliwicz found that the prevailing pattern of space use in Polish populations was mutually exclusive territories of females and extensive overlapping home range of male^[31]. In Qinghai-Tibet Plateau meadow population of the root vole, there was no overlapping home range among adult females, but spatial overlap among males and between male and female^[12]. But recently we found root voles were characterized as maternal clusters in this area (unpublished). Although these findings are different, the root vole has two spatial patterns: maternal cluster, and territorial female. The spatial behavioral plasticity of voles is responsible to habitat fragmentation and kinship^[32~38]. So, the prevailing spatial system of root voles is maternal cluster and male territorial overlapping with several females. It is said that the prevailing mating system of root voles is polygyny.

On the other hand, operational sex ratio is an important factor on variation of the mating system. In natural populations of polygamous *Peromyscus leucopus*, the spatial relationship between males and females changes with the breeding status of females and with males associating of females only in estrus or close to estrus^[39]. According to the fact that females mate polyandrously and males polygynously, and the operational sex ratio is not male-biased nor female-biased in the natural populations, Xia et al. have inferred that the species is only considered to be promiscuity based on genetic evidence^[39].

We can discuss the two findings of spatial system of the root voles based of our laboratory results and with regard to operational sex ratio in natural populations. The operation sex ratio involves in mating chance and is subject to local demography. In the Canada's western Arctic population, there was female-biased operational sex ratio (female/male = 2)^[24]. In the limited and patchy habitats, males which have a tendency to mate polygynously easily access to more than one of estrus females. Contrary, several females which have a tendency to

mate monogamously have to share one male and to adjust their own female spatial relationship to form the maternal clusters. In the Qinghai-Tibet Plateau meadow population, there was equal of operational sex ratio (female/male = 1)^[23]. In this natural condition, we consider that males which have a tendency to mate polygynously must compete to access to many estrus females and have to adjust their spatial relationship to females according of chance of mating. So, It is no wonder that adult males overlapped a little much in home range each other. Recently, we found the root voles became female-biased operational sex ratio in patchy habitats in this area (unpublished). Based upon the fact that females mate monogamously and males mate polygynously in our laboratory study, and the operational sex ratio is female-biased in the natural populations, we should inferred that the root voles is only considered to be polygynous.

3.2 Effect of familiarity on mate choice in polygamy

In mating behavior, intersexual familiarity makes a difference between unfamiliar and familiar individuals^[9]. Many documents have showed that familiarity is one of criteria to compare monogamy to polygamy in microtine with respect to laboratory study^[7]. For example, female prairie voles (*M. ochrogaster*) of monogamy, showed a preference of familiar to unfamiliar males in mate choice as well as males did, while female and male meadow voles (*M. pennsylvanicus*) of promiscuity both had no this similar preference^[20], like montane voles (*M. montanus*)^[13]. Because effect of familiarity on mate choice of polygynous voles has been not studied previously^[5,7], it seems to be the prevailing idea that only do female monogamous voles have the preference for familiar males in mate choice, but not female polygamous voles.

However, our results on mate choice of root voles showed females preferred familiar to unfamiliar males and preferred partner to familiar males in polygynous voles (Table 1, 3, 5). It suggested that effect of familiarity on mate choice of females was short- and long-term in polygynous voles. So, familiarity should be a same criterion to distinguish between polygyny and promiscuity as between polygamy and monogamy in mate choice of microtine.

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中 文 摘 要

根田鼠的熟悉性及其自然动情下的配偶选择

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报道了在室内雌鼠自然动情条件下根田鼠两性个体配偶选择的 3 种熟悉性效应的 5 组实验结果, 包括雌性对熟悉和陌生雄鼠、配偶和陌生雄鼠、配偶和熟悉雄鼠的择偶行为实验, 雄性对熟悉和陌生雌鼠、配偶和陌生雌鼠的择偶行为实验。在实验前, 将 1 对性成熟的雌雄鼠 (非亲缘关系) 每天关养 8 h 共 8 d 建立熟悉性; 配对雌雄鼠至少生育 1 胎则为配偶关系。在 Y 形迷宫内的 30 min 实验中, 两个被选择鼠分别以项链拴在横跨选择箱顶端中央的一根铁丝上, 限制它们在各自箱内活动; 而允许异性选择鼠从中立箱自由进入两个选择箱。记录选择鼠对异性被选择鼠的访问、社会探究、攻击、交配和友好行为的频次和时间。经 Wilcoxon 关联样本 T 检验发现, 除交配行为不显著外, 雌性根田鼠均选择熟悉性较高的雄鼠; 而雄鼠不具这种选择性。该结果提示雌雄根田鼠的不同择偶行为也许就是反映该种婚配制度特征的直接行为过程。因此, 在择偶行为中, 雌性根田鼠表现的单配性倾向和雄鼠的多配性倾向, 只能以其婚配制度为一雄多雌制的假设来解释。我们的实验还说明在多配制田鼠中, 一雄多雌制与混交制在雌鼠择偶行为上是不同的, 而与单配制的相似或相近, 故简单地比较多配制与单配制则不能反映田鼠亚科动物婚配制度的多样性。

关键词: 根田鼠; 配偶选择; 熟悉性; 婚配制度

(上接第 319 页)

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