Intraspecific behavioral variation in two populations of wild-caught Mandarin voles

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Abstract: Small mammals are likely to be able to accommodate to localized environmental shifts through the evolution of alternative behavioral strategies. Intraspecific social systems may vary considerably among populations of a species as a result of changing environmental conditions. This study examined whether behavioral traits of socially monogamous mandarin voles (*Microtus mandarinus*), differed between two populations (Chengcun and Xinzheng) characterized by different environmental features, namely altitude and amount of precipitation. Body mass, anxiety, locomotor activity, and partner preference of the two populations were compared. Females in the Chengcun population were much heavier compared with males. However, Xinzheng males were significantly heavier than Chengcun males. Voles in the Chengcun population spent a significantly longer period of time in the central area of an open field compared with animals in the Xinzheng population, thereby demonstrating less anxiety in the Chengcun population. Results of a partner preference test show that the Xinzheng population displayed a strong preference for unfamiliar conspecifics of the opposite sex, while Chengcun males showed a significant preference for a familiar partner. In addition, Chengcun females stayed in the compartment of an unfamiliar vole for a significantly longer period of time relative to the time they spent in the compartment of familiar vole. However, Chengcun females attacked unfamiliar conspecifics more frequently and for a significantly longer period of time they than did the familiar partner. These data suggest that the two populations show significant differences in body weight, anxiety and partner preference due to geographical variation.

Key words: Anxiety; Geographical variation; Intraspecific variation; Mandarin voles (*Microtus mandarinus*); Partner

棕色田鼠两个地域野生种群的行为比较

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摘要：小型哺乳动物能够通过行为策略的进化适应周围的环境。其中，种内社会组织也可随环境参数的变化而变化。河南灵宝程村气候干燥、海拔高，而新郑则气候湿润、海拔低。来自河南灵宝程村的棕色田鼠种群和来自新郑的种群是否在社会行为、情绪、以及性二型上有所差别，目前还不清楚。本研究中，我们通过旷场实验和熟悉选择试验比较了两个种群的情绪、运动能力以及对熟悉鼠和陌生鼠的选择。统计结果表明，程村种群的雌性个体比雄性个体重，而新郑种群的雄性体重比程村种群的重。在旷场实验中，程村种群比新郑种群表现出较多的焦虑样行为。配偶选择实验中，新郑种群不论雌雄都表现出了对陌生异性的喜好。程村种群雄性则更愿意选择熟悉的个体。而且，程村的雌性待在陌生箱攻击陌生鼠的时间远大于熟悉鼠。以上结果表明，两个野生种群在体重、情绪以及对熟悉鼠和陌生鼠选择上都表现出了明显的种群间差异。

关键词：种内变异；棕色田鼠；性二型；熟悉性选择；情绪
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1 Introduction

Intraspecific behavioral variation provides an opportunity to examine the origins of behavior. Characterization of behavioral differences among geographically disjunct populations can be used to test hypotheses on the evolution of social behavior and/or to identify patterns of inheritance that regulate these behaviors (Roberts *et al.*, 1998a). Since geographical variation in behavior may evolve over relatively short time frames (Riechert, 1999), studies of intraspecific variation in behavior can provide excellent opportunities to study the proximate and ultimate bases for behavioral adaptation (Lott, 1991).

Although population and quantitative genetic studies have demonstrated adaptive geographical variation

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in non-behavioral traits (Foster, 1999), there is a limited body of literature on geographical variation in behavioral traits. Nevertheless, such studies may offer the best hope for elucidating behavioral adaptations (Arnold,1992; Foster,1999). For example, previous studies have found that feral ass (*Equus africanus*) populations in arid and mesic environments exhibited intraspecific variation in mating system and social organization (Emlen and Oring, 1977; Moehlman, 1998); wolf spiders exhibited geographical variation in dispersal behavior in relation to landscape structure (Bonte *et al.*, 2006) and both red foxes (*Vulpes vulpes*) and Arctic foxes (*Alopex lagopus*), show intraspecific variation in mating system and group structure as a result of differences in food and other resources (Macpherson, 1969; Macdonald, 1983; Hersteinsson, 1984; Moehlman, 1989). However, few studies have been done on geographical variations in partner preference and anxiety.

Previous researches on prairie voles (*Microtus ochrogaster*) from eastern Kansas (KAN) and Illinois (LL) h ve fo nd si nifi ant i terp pula ion v riat on i sexu l dim rphi m, pa tner preference (Roberts *et al.*,1998a) and receptivity (Roberts *et al.*, 1998b). Prairie voles from ILL are less sexually dimorphic in body size, more likely to show alloparenting toward pups (Roberts *et al.*,1998a), more aggressive toward intruders (Lee, 1996), and less exploratory (Dharmadhikari *et al.*, 1997) than conspecifics from KAN. Roberts *et al.* (1998b) found that differences also exist in reproductive strategies and social systems.

Anxiety is an important component of social behavior. For example, in a previous study using the elevated plus maze (EPM) test, male prairie voles were found to enter the open arms of the EPM more frequently and remained there significantly longer showing less anxiety and a higher level of overall locomotor activity than did male meadow voles (*Microtus pennsylvanicus*) (Stowe *et al.*, 2005). This result suggests that the social environment may differentially influence anxiety of closely related vole species with different life strategies. It is also inferred that anxiety associated with social behavior may also show geographical variation.

Microtus species have complex social behaviors and have been used to study adaptations to naturally occurring environmental variation (Wolff, 1985). The mandarin vole (*Microtus mandarinus*) is a socially monogamous rodent that is widely distributed in China (Tai and wang,2001; Tai *et al.*,2001). This species offers an interesting model for the study of geographical adaptation of social behavior. However, it is not clear whether mandarin voles show significant geographical variations in behaviors. Weather condition and altitude in Xinzheng and Chenchun are significantly different. It is hypothesized that mandarin vole populations from these two areas differ in their behaviors. The purpose of this study was to compare body weight, anxiety, locomotor activity, partner preference between the two populations of wild-caught mandarin voles.

2　Animals and methods

2.1　Animals and housing conditions

Mandarin voles for this study were captured from two areas in Henan Province, Chengcun town and Xingzheng city. Chengcun town has an altitude of 650 m and is located on a loessial altiplano (34°41′ N and 111°11′ E). Its average annual temperature is 13 – 13.8℃ with a significantly difference between day and night. The annual rainfall is 500 – 600 mm (Tai and Wang,1998). Recently, we found another population of mandarin voles in central Henan Province, Xinzheng city which is 300 kilometers away from Chencun town and has an altitude of 193 m. Xinzheng (34°16′–34°39′ N and 113°30′–113°54′ E) has an average annual temperature of 14.4℃ and annual rainfall of 676.1 mm.

Population densities were investigated from five sample squares of each area. Animals caught were maintained on a 12-h light: 12-h dark cycle and allowed free access to food (carrot and rabbit chow), water and cotton for nesting material in polycarbonate cages (44 cm × 22 cm × 16 cm). To facilitate habituation to our colony room and to minimize influence of stress following transport from field sites, a one-week acclimatization period was included before all experimental test. All the procedures were approved by the Animal Care and Use committee of Shaanxi Normal University and were in accordance with the Guide for the Care and Use of Laboratory Animals of China.

2.2　Body weight

We compared body weight between sexes and populations for all non-pregnant full size adults (Chengcun: $N = 16$ and 23 for females and males, respectively; Xinzheng: 11 and 10 for females and males, respectively).

2.3　Open field test (OFT)

Locomotor activity (Swiergiel and Dunn, 2007) and anxiety reactivity (Anderson and Hughes, 2008) were quantified for 5 min in an open field, a Plexiglas box (50 cm × 50 cm with a white floor divided into 16 squares and surrounded by a 25 cm high black wall). The four central squares were defined as the center and the 12 squares along the wall as the periphery (Swiergiel and Dunn, 2007). The arena was illuminated with one 25 W red bulb above the center of the field (Brenes *et al.*, 2008). Light intensity was approximately 200 lux (Marques *et al.*, 2008). Eight males and eight females of each population were tested in open field. Every vole was tested only once in this test. All behavioral tests were conducted between 3 p. m. to 5 p. m. Each vole was gently placed in the centre of the box. behaviors were recorded for 5 min by a camera placed above the apparatus and scored later by an experimentally blind rater, using Noldus Observe 5.0 software (Noldus, The Netherlands). After each test the arena was cleaned with 70% alcohol solution. The frequency and time spent in central and peripheral zones and the total transitions were scored and analyzed by Noldus Observe 5.0 software (Noldus, The Netherlands).

2.4 Partner preferences

Experimental animals were full adults (N = 8 pairs per population). We assigned females randomly to a malepartner and allowed the pair to cohabit for 72 h prior to preference test. For testing, the experimental animals were placed in a Y-shaped test apparatus consisting of three polycarbonate chambers (20 cm × 25 cm × 45 cm). Two of the cages (stimulus) were placed in parallel with a third cage (neutral) attached separately to each stimulus cage by a plastic tube (15 cm in length and 7.5 cm in diameter) (Williams *et al.*, 1994). The two parallel chambers housed the "partner" and the "stranger" voles (mandarin voles similar in sex, age, social history, and weight to the partner, but unfamiliar to the test animal). The additional animals were used as strangers. The stimulus animals were choosed before the behavior test. A gonadally intact male and an estrous female were used as stimulus animals. At the beginning of the test, the test animal was placed in the neutral cage with free access to the whole apparatus to habituate for 10 min. Then, the plastic tubes were blocked to keep the test vole in neutral cage before the partner and stranger were loosely tethered within their separate cages. After 10 min habituation, blockages were removed. behaviors were recorded for 30 min using a digital video camera and scored later by an experimentally blind rater, using Noldus Observe 5.0 software (Noldus, The Netherlands). Time in physical contact, aggression and amicable behaviors to the stranger and the partner were scored and analyzed (Jia *et al.*, 2008).

2.5 Statistical methods

The normality of variables was tested using one-sample Kolmogorov-Smirnov test. Almost all the behavior results were normally distributed, except the duration of aggressive behavior.

Data for body weight and population densities in two regions were analyzed by Independent-samples T-test. Open field tests were analyzed by two-way analysis of variance (ANOVA) using population and sex as factors. Statistical analysis was done with a paired t test or 2 related samples of nonparametric Wilcoxon tests (according normality of data) to compare the duration of physical contact and aggression with the partner versus the stranger. All tests were two-tailed. Comparisons were considered statistically significant at $P < 0.05$.

3 Results

3.1 Body weight and population density

Independent-samples T-test (Fig. 1) revealed that females from Chengcun were significantly heavier than males (female: 37.16 ± 1.26 g; male: 30.59 ± 0.69 g; $t_{37} = 4.93$, $P < 0.01$). There was no significant sexual dimorphism in Xinzheng population with respect to body weight (female: 35.04 ± 0.98 g; male: 34.96 ± 0.34 g; $t_{19} = 0.05$, $P > 0.05$). The Xinzheng males were significantly heavier than Chengcun males ($t_{31} = 3.20$, $P < 0.01$), but there was no significant difference between the weight of Chengcun and Xinzheng females ($t_{25} = 1.23$, $P > 0.05$).

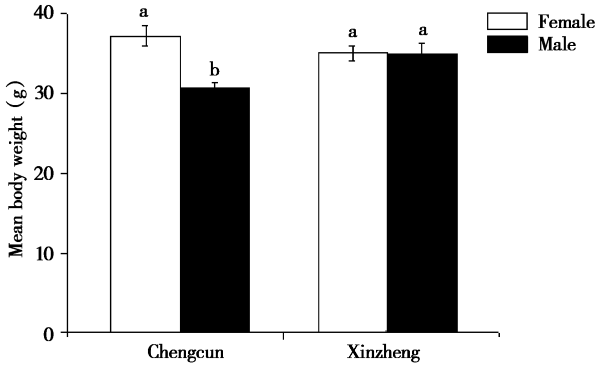

Fig. 1 Differences in body weights in male and female Mandarin voles from Chengcun and Xinzheng. Groups with same letters were no significantly different. (ab: $P < 0.01$). Error bars represent SEMs.

Furthermore, the population densities were different in the two regions (Independent-samples T-test: t_8 = 128.557, $P < 0.01$; Fig. 2). According to our examination of the two areas, the density of Chengcun is 36.00 ± 0.71 mandarin voles per hectare, while the density in Xinzheng is 142.40 ± 0.43 mandarin voles per hectare.

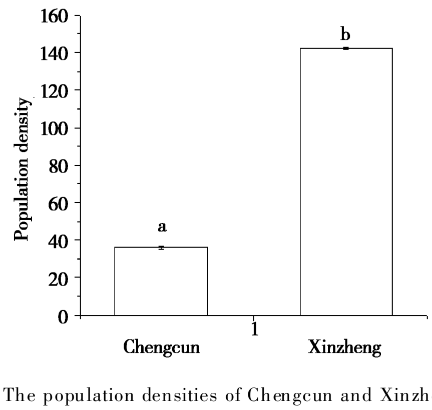

Fig. 2 The population densities of Chengcun and Xinzheng. groups with same letters were no significantly different. (ab: $P < 0.01$). Error bars represent SEMs.

3.2 Open-field activity

The interaction between sex and population exhibited no significant effect on the percentage of time in the central area ($F_{1,28} = 0.13$, $P > 0.05$). The main effects of both population and sex were significant (population: $F_{1,28} = 12.07$, $P < 0.01$; sex: $F_{1,28} = 15.25$, $P < 0.01$).

Independent-samples *T*-test (Fig. 3A) revealed that the females of both populations spent more time in the central area than did males of the same population (Chengcun: $t_{14} = 2.47$, $P < 0.05$; Xinzheng: $t_{15} = 3.79$, $P < 0.01$). Further, Xinzheng males spent less time in the central area than Chengcun males ($t_{15} = 3.46$, $P < 0.05$).

The interaction between sex and population showed no significant effect on the total transitions ($F_{1,28} = 1.84$, $P > 0.05$). The effect of sex was significant ($F_{1,28} = 6.06$, $P < 0.05$), with males having more transitions. However, the effect of population was no significant on total transitions ($F_{1,28} = 2.21$, $P > 0.05$). Independent-samples *T* test (Fig. 3B) showed that Xinzheng males exhibited a significant difference from Xinzheng females in the total transitions ($t_{15} = 3.33$, $P < 0.01$).

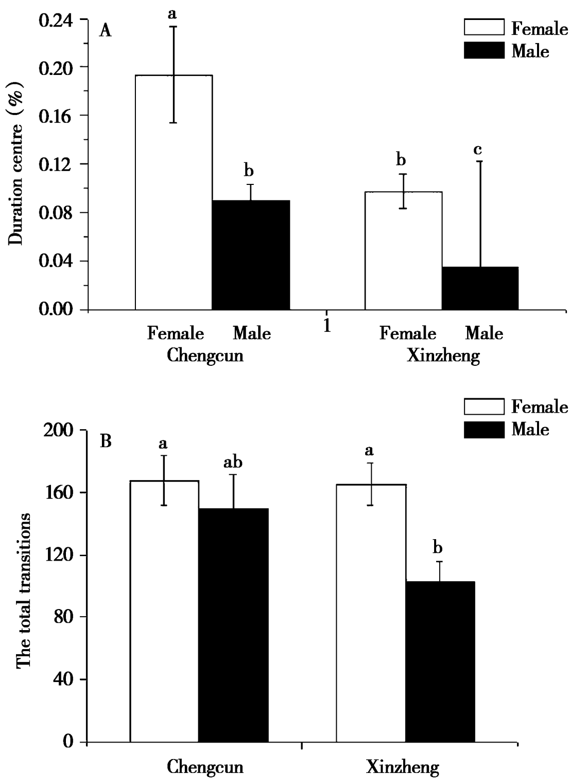

Fig. 3　The time in central area and total transitions of mandarin voles from two populations in Open field tests. Groups with same letters were no significantly different. ($P < 0.05$). A : Time in central area; B : Total transitions. Error bars represent SEMs.

3.3　Partner preferences

Chengcun males spent significantly more time in the compartment of familiar vole than in the compartment of stranger vole, showing a significant preference

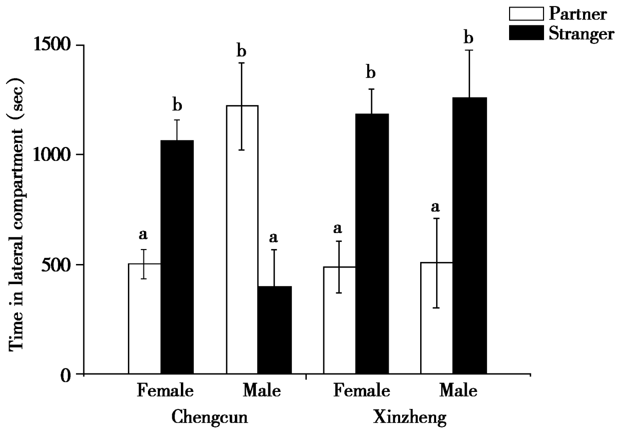

Fig. 4　The time in lateral compartment of the partner preference test. Within all groups, in addition to Chengcun males, other animals spent significantly more time with the stranger versus a familiar partner. Groups with same letters were no significantly different. ($P < 0.05$). Error bars represent SEMs.

for the familiar partner ($t_7 = 3.15$, $P < 0.05$; Fig. 4). However, Chengcun females spent more time in the stranger compartment ($t_7 = 5.08$, $P < 0.01$), as did both males and females from Xinzheng (female: $t_7 = 4.06$, $P < 0.01$; male: $t_7 = 2.58$, $P < 0.05$). Although, Chengcun females spent significantly more time with the stranger, they also displayed more aggressive behaviors to these strangers relative to the partner frequency: $t_7 = 2.78$, $P < 0.05$; Fig. 5A; duration: $Z = 2.38$, $P = 0.02$; Fig. 5B). Xinzheng males and females did not show significant differences in aggressive behavior toward the partner and the stranger (males: duration: $t_7 = 1.64$, $P > 0.05$; frequency: $t_7 = 1.61$, $P > 0.05$; females: duration: $t_7 = 1.04$, $P > 0.05$; frequency: $t_7 = 0.99$, $P > 0.05$). On the other hand, Chengcun males exhibited significantly more amicable behavior with familiar partners ($t_7 = 4.37$, $P < 0.01$) while Xinzheng male and female showed amicable behavior more frequently with strangers (female: $t_7 = 2.32$, $P < 0.05$; male: $t_7 = 2.68$, $P < 0.05$; Fig. 5C). Male mandarin voles from Chengcun population spent more time in amicable behavior with their familiar partners, while mandarin voles from Xinzheng population spent more time in amicable behavior with the strangers although significant differences were not found between them (Fig. 5D).

4　Discussion

The first interesting finding is that Chengcun females were significantly heavier than Chengcun males which may be different from a previous report (Tai *et al.*, 2001). In addition, Xinzheng males were significantly heavier than Chengcun males. This may be due to sexual selection. Sexual selection via male-male competition or female choice favours larger male size in several birds and mammals (Webster, 1992; Mitani *et al.*, 1996; Dunn *et al.*, 2001; McElligott *et al.*,

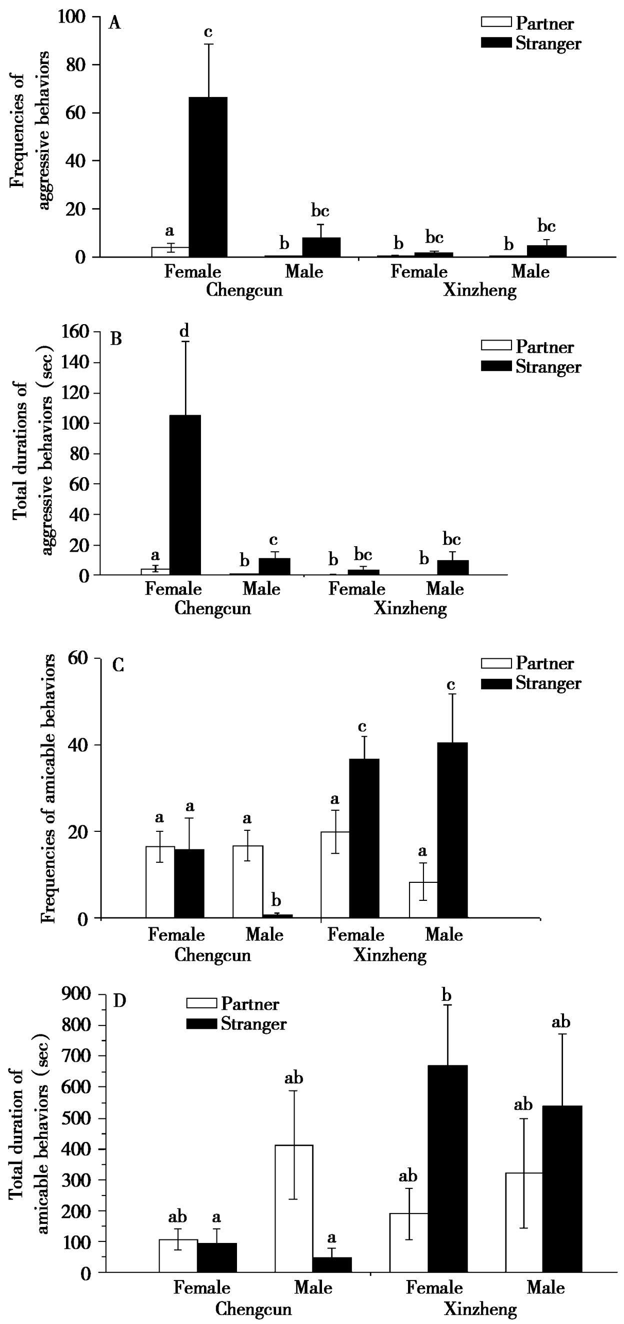

Fig. 5 Behavioral performance in the partner preference test. A and B show frequencies and total durations of aggressive behaviors. C and D show frequencies and total durations of amicable behaviors. Groups with same letters were no significantly different. (P < 0.05). Error bars represent SEMs.

2001; Lindenfors *et al.*, 2003). Thus, an increase in body size may be particularly advantageous to males in polygynous species (Clutton-Brock and Harvey, 1977; Owens and Hartley, 1998), for which the intensity of sexual selection is greater because of increased competition between males over females (Raihani *et al.*, 2006). So we presumed that Xinzheng male voles have greater intensity of sexual selection than Chengchun male because of heavier body weight in the former.

The second finding is that Chengcun voles spent more time in the central area of the open field than did Xinzheng voles. Furthermore, females of the two populations spent more time in the central area than did males. Thus, Chengcun voles appeared to have a lower anxiety level than Xinzheng voles. Open-field tests have been a popular way of assessing emotional reactivity in rats for over 70 years (Hall, 1934; Walsh and Cummins, 1976; Brain and Marrow, 1999). Xinzheng males had the least total transitions. Therefore, they showed significantly less locomotion. But Xinzheng females presented more locomotion than Xinzheng males. There was no difference in total transitions between the two populations that showed locomotion activities in the present study. So we believe that the anxiety of voles did not effect their locomotion activities. Other researches indicate a neural circuit involved in mediating anxiety-associated behavior in voles, and that the functioning of this circuit is differentially influenced by social environment between social and non-social species (Stowe *et al.*, 2005). Stowe *et al.* (2005) found that male prairie voles had a higher level of overall locomotor activity than did male meadow voles. In addition, male prairie voles were found to enter the open arms of the EPM more frequently and remained there for a significantly longer period of time showing less anxiety and a higher level of overall locomotor activity than male meadow voles (Stowe *et al.*, 2005). In terms of anxiety, our result indicates that Chengcun population showed anxiety like social prairie voles while Xinzheng population were like non-social meadow voles.

The third interesting finding is that Xinzheng males and females showed a significant preference for strangers, while Chengcun males showed significant preferences to familiar partners. Chengcun females showed significantly more aggressive behavior toward strangers than toward familiar partners. Longer duration of aggressive behavior to the stranger may not only reduce the time in familiar parther's compartment, but also decrease the amicable behavior to the familiar partner. It is inferred that Chengchun females may also show preference toward the familiar partner. Preference for spending time with a mate versus with a stranger, that is, partner preference, by monogamous species but not by polygynous species of *Microtus* was first demonstrated by Dewsbury and colleagues (Webster *et al.*, 1982; Shapiro *et al.*, 1986; Roberts *et al.*, 1998a). Pair bonding is also a theoretical construct that involves not only selective aggression and affiliation but also other behaviors, but these behaviors may be necessary (if not sufficient) for the development of a monogamous bond (Insel *et al.*, 1995). Our results suggest that Chengcun males and females might be able to form partner preferences after 72 h of cohabitation, while Xinzheng population was not able to form such preferences under the same condition.

Small rodents with high reproductive potential often live in seasonally and socially unpredictable habitats and, consequently, have flexible social systems to best accommodate variable ecological circumstances (Eisenberg, 1966; Parker *et al.*, 2001). They frequently display intraspecific variation in social organization (Parker *et al.*, 2001). For example, typically monogamous prairie voles have a polygynous mating system during the winter breeding season and under high population densities in east-central Illinois (Getz *et al.*, 1987; McGuire *et al.*, 1993), and habitually show polygyny in the more xeric habitat of eastern Kansas (Fitch, 1957; Roberts *et al.*, 1998a). This social system is thought to evolve when males are unable to monopolize more than one female, either because females are highly dispersed (Kleiman, 1981; Runcie, 2000) or because males are unable to defend home ranges large enough to accommodate more than one female (Gosling, 1986; Runcie, 2000). Several factors including body size (Moehlman, 1989) and resource availability are suggested to contribute to the variation of mating systems among canid species (Geffen *et al.*, 1996; Kamler *et al.*, 2004). In central Xinzheng city, mandarin voles occupy a moist habitat with abundant food resources. In contrast, mandarin voles in Chengcun town occupy a drier habitat and less abundant food resources. Food availability, habitat availability and resource dispersion have been suggested as major factors contributing to intraspecific variation in reproductive strategies and group structure in canids (Macdonald, 1983; Geffen *et al.*, 1996; Kamler *et al.*, 2004). Based on our field research, the density of Chengcun population was lower than Xinzheng population. Chengcun individuals were relatively dispersed, while, Xinzheng individuals were concentrated. When the food and partners are distributed uniformly or highly disperse, the animals will display monogamy. Whereas, when the food and partners densely distributed, the animals will display polygyny (Zhang and Zhang, 2003). Our conclusions may be supported by previous reports that nonmonogamous and asocial montane voles can form extended maternal families (Jannett, 1978) or polygynous mating systems (Jannett, 1980) under high population densities, and engage in facultative monogamy under low-density conditions (Jannett, 1980; Berger *et al.*, 1997). California voles also exhibited a monogamous mating system under low densities, but under the high densities, they were polygynous (Lidicker, 1980). So under high population density, Xinzheng voles probably showed non-monogamous characteristics on behaviors, while the Chengchun population exhibited monogamous characteristics on behaviors under low population density.

In conclusion, the intraspecific behavioral variation indeed occurred in the two populations of wild-caught mandarin voles. The population from Chengcun had lower male body weight and less anxiety than did the Xinzheng population. The Chengcun population also formed significant partner preferences, while the Xinzheng population did not. Our results for body weight, open field test and partner preference test show that Chengcun population demonstrated socially monogamous characteristics, but Xinzheng population displayed nonmonogamous traits. We inferred that this may be caused by environmental factors. The different annual rainfall may influence food distribution, and furthermore, food distribution may affect population densities. Population density is associated with social organization. So the two populations displayed behaviors characteristic of different mating systems and social organizations.

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