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RESEARCH ARTICLE

Partner Preference and Mating System of the Taiwan Field Vole (*Microtus kikuchii*)

Chia-Chien Lee[1], Chih-Hsien Chiu[2], Liang-Kung Lin[3] and Y. Kirk Lin[1,4*]

1. Institute of Ecology and Evolutionary Biology, National Taiwan University, Number 1, Section 4, Roosevelt Road, Taipei City 10617, Taiwan (R.O.C.).
2. Department of Animal Science and Technology, National Taiwan University, Number 1, Section 4, Roosevelt Road, Taipei City 10617, Taiwan (R.O.C.).
3. Department of Life Science, Tunghai University, Number 1727, Section 4, Taiwan Avenue, Taichung City 40704, Taiwan (R.O.C.).
4. Department of Life Science, National Taiwan University, Number 1, Section 4, Roosevelt Road, Taipei City 10617, Taiwan (R.O.C.).
** Corresponding author. Tel.: 02-33664534; Email: kirklin@ntu.edu.tw*

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ABSTRACT: The mating system of the Taiwan field vole (*Microtus kikuchii*) has been proposed to be monogamous. In monogamous animals, individuals should exhibit monogamy syndromes, such as little sexual dimorphism and strong pair bonding (a strong social preference for a familiar partner versus a strange one). In this study, we examined the effect of cohabitation on the partner preference. In a reciprocal experiment, all test individuals were cohabited with a heterosexual vole for 24 hr prior to the partner preference trials. We collected the feces of voles before and after the trials, and analyzed the concentration of fecal steroid hormones, including testosterone of males, progesterone and estradiol of females, and corticosterone of all voles. The results showed that the behaviors of focal voles were not influenced by the status (partner or stranger) of stimulus vole. There was no significant relationship between steroid hormones and partner preference. Furthermore, the degree of sexual dimorphism in the Taiwan field vole was low, and similar to that of the monogamous prairie vole (*M. ochrogaster*). In light of this study and other recent findings, we propose that the mating system of the Taiwan field vole is not strictly monogamy, but flexible depending on environmental conditions.

KEY WORDS: EIA, mating system, partner preference test, steroid hormone, sexual dimorphism, Taiwan field vole.

INTRODUCTION

A mating system is the way in which an animal society is structured in relation to sexual behavior. Mating systems in mammals can be generally classified as monogamy, polygyny, polyandry, or promiscuity based on the number of mates that each adult individual has (Wittenberger, 1979; Clutton-Brock, 1989). Monogamy, defined as a long-term association, and essentially exclusive mating relationship, between one male and one female occurs in less than 3% of mammalian species (Kleiman, 1977; Wittenberger and Tilson, 1980; Carter and Getz, 1993). Some examples are: common marmosets (*Callithrix jacchus*, Evans, 1983), cotton-top tamarins (*Saguinus oedipus*, Price and McGrew, 1991), and prairie voles (*Microtus ochrogaster*, Thomas and Birney, 1979; Getz *et al*., 1981). Monogamous mammalian species exhibit a variety of life histories. Not a single ecological mechanism could fully explain the occurrence of monogamy in all mammalian species. However, a list of characteristics has been proposed (Kleiman, 1977; Carter and Getz, 1993; Carter *et al*., 1995) to determine if monogamy occurred. In a population with predominantly monogamy, one would observe at least some of the following monogamy syndromes:

1. Little or no sexual dimorphism in morphology, compared to related species of other mating systems (Dewsbury *et al*., 1980; Heske and Ostfeld, 1990; Boonstra *et al*., 1993; Ostfeld and Heske, 1993);
2. Long-term pair bonding persists throughout breeding and non-breeding seasons (Carter *et al*., 1995);
3. Display aggressive behaviors by both sexes toward unfamiliar conspecifics for defending the nest and territory (Carter and Getz, 1993; Carter *et al*., 1995; Back *et al*., 2002);
4. Home ranges overlap between only one male and one female, and range sizes are similar (Gaulin and FitzGerald, 1988; Reichard, 2003; Wu *et al*., 2012);
5. High paternal investment, compared to related species of other mating systems (Oliveras and Novak, 1986; Solomon, 1993; Patris and Baudoin, 2000);
6. Show incest avoidance and reproductive suppression

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by adult individuals within a family group (Carter *et al*., 1995);
7. Social factors regulate reproductive physiology (e.g., estrus induction and ovulation) (Taylor *et al*., 1992; Carter *et al*., 1995).

Forming long-term heterosexual pair bonds is a pivotal characteristic among monogamous animals. Pair bonding represents an intense social attachment between one male and one female (DeVries *et al*., 1995; Carter *et al*., 1997). For small mammals, the observation and quantification of pair bonding could rarely be assessed directly in the field. Researchers often use spacial relationships (home range overlaps) of animals via live-trapping or radio-telemetry to indirectly infer whether there is bonding between one male and one female (Getz *et al*., 1981; Getz and Hofmann, 1986; Jike *et al*., 1988). Laboratory studies could support field information. Researchers can use the partner preference test to investigate whether pair-bonding occurs (Pierce and Dewsbury, 1991; Williams *et al*., 1992; Winslow *et al*., 1993). In addition, genetic analyses, specifically paternity assignments, of field populations could provide further information on genetic mating system. In a monogamous system, the incidence of multiple paternity should be very low (Lin *et al*., 2009; Wu *et al*., 2012).

Pair-bonding involves two major categories of animal hormones: neuropeptides and steroids. Neuropeptides including oxytocin and arginine vasopressin, have been confirmed to maintain the long-term bonding of male and female mammals (Insel and Hulihan, 1995; Insel *et al*., 1998; Young *et al*., 1998; Cho *et al*., 1999; Young and Wang, 2004). When the concentration of neuropeptides is high, the focal animal would show greater partner preference (Williams and Carter, 1992; Winslow *et al*., 1993; Williams *et al*., 1994; Cho *et al*., 1999). In contrast, when the receptors of neuropeptides are inhibited, a monogamous animal would not exhibit partner preference (Winslow *et al*., 1993; Liu *et al*., 2001). On the other hand, steroids are synthesized from two classes of endocrine glands, the gonads and adrenal glands. The gonadal steroids, such as progesterone, estradiol, and testosterone, are related to reproductive behaviors and parental care, while the adrenal steroid hormones, such as cortisol, corticosterone, and adrenaline, secreted by adrenal cortex, are related to homeostasis and stress. Previous studies (Carter *et al*., 1995; Carter *et al*., 1997) have shown differential effects of the two classes of steroid hormones on pair bonding of male and female mammals, e,g., there was no difference in partner preference between intact vs. gonadectomized individuals (DeVries *et al*., 1997). Furthermore, mating could not facilitate partner preference formation in 24-hr or longer cohabitation periods (Williams *et al*., 1992). Thus partner preferences could develop in the absence of gonadal hormones. In naïve prairie voles, the effects of corticosterone on partner preferences were sexually dimorphic (DeVries *et al*., 1995; DeVries *et al*., 1996; Carter *et al*., 1997). In males, exposure to either the stress (swimming) or corticosterone (exogenous injections) facilitated the development of pair-bonding. Conversely, adrenalectomy inhibited partner preference formation in males and the effects of adrenalectomy could be reversed by corticosterone replacement. In contrast, in females, stress or corticosterone inhibited the formation of partner preferences, while adrenalectomized females formed preferences more quickly than intact controls.

The prairie voles, a model species in the study of the mammalian mating system, have been categorized as monogamy (Thomas and Birney, 1979; Getz *et al*., 1981) based on previous studies in ecology, behavior, physiology, genetics and neurobiology (Getz *et al*., 1981; Insel and Shapiro, 1992; Getz *et al*., 1993; Winslow *et al*., 1993; Carter *et al*., 1995; Lim *et al*., 2004). The species has little sexual dimorphism in body size, compared to related species of other mating systems (Dewsbury *et al*., 1980). In the laboratory, a prairie vole previously paired with a partner, when given the choice of spending time with the partner vs. a stranger individual, often spent much more time with its previous partner (Pierce and Dewsbury, 1991; Insel *et al*., 1995). In contrast, a similar microtine species, meadow voles (*M. pennsylvanicus*), do not exhibit such partner preferences (Lim *et al*., 2004). The mating system of the latter species has been categorized as promiscuity (Madison, 1980; Gruder-Adams and Getz, 1985). Studies (e.g., Lim *et al*., 2004) on neuropeptides of the prairie voles showed that individuals with higher concentration of oxytocin and vasopressin performed significantly greater partner preference than other individuals. The densities of oxytocin and vasopressin receptors in the ventral forebrain of prairie vole are also significantly higher than other microtine species, such as meadow voles (*Microtus pennsylvanicus*) and montane voles (*Microtus montanus*), both with non-monogamy mating systems (Insel and Shapiro, 1992; Insel *et al*., 1994; Young *et al*., 1998; Lim *et al*., 2004). On the other hand, in the study of steroid hormones in prairie voles, gonadal steroid hormones had no significant effect on partner preference. Whereas the effects of adrenal steroid hormone, corticosterone, was sex-dependent. It could increase males' partner preference, but had an opposite effect on females (DeVries *et al*., 1995; DeVries *et al*., 1996; Carter *et al*., 1997).

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The Taiwan field vole (*Microtus kikuchii*) is an endemic species in Taiwan, distributed in high mountains at >2,500 meters in altitude. Thus far, field and laboratory studies have supported the proposition that the mating system of the Taiwan field vole is monogamy (Wu, 1998; Yang, 2011; Wu *et al*., 2012). The home range sizes of adults did not significantly differ between sexes in different seasons. The home range of more than 70% of males or females showed overlap with that of only one opposite sex (Wu, 1998; Wu *et al*., 2012). In addition, microsatellite DNA information suggested that a vole mated exclusively with the same heterosexual individual in a breeding season (Wu *et al*., 2012). In a partner preference experiment, Chen *et al.* (2006) found that the Taiwan field vole, after a 3-month pairing period, spent significantly more time contacting with the paired partner than with an unfamiliar individual. Yang (2011) showed that male voles would provide direct care that enhanced growth, development and locomotion ability of pups, and improve the survival rate of offspring in a low temperature environment.

However, new information from several recent studies on the Taiwan field vole (Quan *et al*., 2010; Liang, 2012; Chappell *et al*., in review) prompted us to re-examine past evidence and reconsider the mating system of the species. First, the home range results laid out in Wu *et al*. (2012) did show overlaps between more than one male and female pairs in 30% cases. In addition, the trap spacing was 20-m and trapping interval 1-month in the study, which may underestimate population density and the degree of home range overlaps among individuals. In contrast, Quan *et al*. (2010) in a 6-week intensive (nearly daily) trapping study found extensive home range overlaps among multiple adult males and females at a forest site. Second, a study by Liang (2012) showed that trapping at nest sites often capture more than one pair of adults particular during the early breeding season. Both studies (Quan *et al*., 2010; Liang, 2012) indicated that more than one male and female adult would at least sometimes overlap extensively in home ranges. Third, the partner preference experiment by Chen *et al*. (2006) used a 3-month pre-trial cohabitation. The length of cohabitation may be too long and problematic. Parker *et al*. (2001) pointed out that long-term cohabitation could generate partner preference even in a non-monogamous species. In the monogamous prairie vole, Williams *et al*. (1992) showed that 24-hr cohabitation is sufficient to generate partner preference. Four, the neuroanatomy data (Chappell *et al*., in review) showed that Taiwan field voles had unique receptor expression that was different from that of prairie voles. Oxytocin binding in the nucleus accumbens is important for forming pair bonds in female voles; however, the receptor levels were low in the Taiwan field vole. Finally, although monogamous breeding produces single paternity litters, finding single paternity does not indicate that the mating system is monogamy. Wu *et al*. (2012) did not find multiple paternity in the Taiwan field vole. It could be due to other reason than monogamy. First of all, the litter size of the species is small (mostly 1–2 pups per litter). The chances of finding multiple paternity within a litter are low even if females mated with multiple females. Furthermore, female voles may mate with multiple males, and choose one male's sperm to sire her young through cryptic choice (Eberhard, 1996).

Based on the above arguments, we think that additional supports are needed to establish that the Taiwan field vole is monogamous. Previous studies related to the mating system of the Taiwan field vole focused on item 4 and 5 of the monogamy syndromes. In this study we aimed to examine items 1 – 3. We used partner preference experiments with 24-hr cohabitation to examine pair-bonding (item 2) and aggressive behavior (item 3). We compared the sexual dimorphism (item 1) in Taiwan field vole body weight with those of other microtine species (Dewsbury *et al*., 1980) to provide new evidence for the mating system of the Taiwan field vole. Finally, as we mentioned earlier, neuropeptide and steroid hormones may affect pair bonding. Because the effects of those hormones had not been examined in relation to partner preference in the Taiwan field vole, we did so in this study. We investigated if the gonadal hormones (progesterone and estradiol) of female voles had effect on partner preferences of male voles; if the gonadal hormone (testosterone) of male voles had effect on partner preferences of female voles; and, if the corticosterone had positive effects on male partner preference and negative effects on female partner preference.

MATERIALS AND METHODS

Voles and breeding colony

Taiwan field voles (*Microtus kikuchii*) used in this study were laboratory-bred F1 or F2 generations originated from wild stock trapped from an alpine meadow (24°08'36.4"N, 121°17'17.4"E) at the He-huan Mountains. All voles, except breeding pairs, were housed individually in polycarbonate cages (46 × 25 × 20 cm^3) with 5-cm-thick aspen chip bedding (TAPVEI) and a 15-cm PVC tube as refuge. The breeding colony was maintained at 17 ± 0.5 °C room temperature, and on a 14:10-hr light/dark cycle (lights on at 0700 hour). Sweet potatoes, rodent chow (LabDiet 5001), and water were provided *ad libitum*. Pups remained with their parents until 45 days of age, and were sexed and housed individually until testing. We

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recorded baseline information of each vole (body weight and condition) weekly and breeding pair (litter size at birth, sex ratio at weaning-45 days of age) in the colony.

Sexual dimorphism in body weight

We examined the sexual dimorphism in body weight using the information collected from litters containing at least one male and one female. We used the mean body weight between 90 and 180 days of age of each young to be comparable with other species described in Dewsbury *et al*. (1980), and excluded the weight during the partner preference trials (see below). We obtained information from 8 litters that included 11 males and 10 females.

Partner preference trials

Testing apparatus

The partner preference testing apparatus is made of 0.5-cm thick transparent acrylic (135 × 25 × 50 cm^3, L×W×H), and consists of three equal-sized chambers (45 × 25 × 50 cm^3, L×W×H) divided by the same acrylic material. The two dividers each has a 7 × 7-cm passage hole that allow focal animal to move around chambers freely. At each end of the apparatus, a metal hook fixture allows tether anchoring. Before each partner preference test, we placed new woodchip bedding and two rodent chow pellets in each chamber. A water-bottle was attached on the wall of each chamber. After each test, the apparatus was rinsed with 70% ethanol and scrubbed thoroughly with water to eliminate odors from previous test.

Partner preference tests

Each trial contained four periods: pre-test (5 days), cohabitation (24 hours), preference test (3 hours), and post-test (4 days) periods. All experimental voles were sexually naïve, and were tested at approximately 80 days of age. For a male's partner preference test, one male (focal animal) and two female (one partner and one stranger, stimulus voles) non-related adult voles were included. A female's partner preference test would follow the same methods except that one female and two male non-related adult voles were included. In the pre-test period, the three voles were housed individually. We collected fecal pellets of each vole daily in the morning for 5 consecutive days. On the fifth morning, the focal male and a randomly chosen female (partner) from the duo were placed in a new cage and cohabitated for 24 hours. The remaining female (stranger) was moved to a new cage alone. On the sixth morning, the three animals would be moved to a behavioral testing room before the partner preference test started.

At the start of a test, the partner and stranger were tethered and anchored to the opposite ends of the testing apparatus. The tethered voles acclimated in their respective chambers for 30 min before we introduced the focal vole. The focal vole was placed in the neutral (center) chamber and allowed to move freely in the apparatus. The behaviors of the three voles were video-recorded (Sony HDR-SR12) for 3-hr. At the end of 3 hours, the three voles were separated, and housed individually in the animal colony. Their fecal pellets were collected for the following 4 days in the morning. We condensed each 3-hr video using a 12:1 ratio speed transformation, and watched the full 15-minute videos. We recorded the following 3 behaviors of the focal voles: time in each chamber, time in physical (side-by-side) contact with each vole, and frequency of aggression toward each vole. An aggressive behavior occurred when the focal vole attacked, bit, or chased a stimulus vole (Ferkin, 1988; Williams *et al*., 1992). We determined the choice (prefer-or-not) of the focal vole. A preferred individual was defined as the one (partner vs. stranger) with whom more time was spent by the focal vole in physical contact.

Because the breeding of voles had not been productive, we used a method suggested by Lim *et al*. (2007) to reduce the number of animals required for trials. In those cases (8 cases for males; 4 cases for females), we performed two partner preference tests in one day, one in the morning and the other in the afternoon. The partner vole from the morning session would serve as the stranger vole in the afternoon, and vice versa. Lim *et al*. (2007) showed that there was no measurable test order effect using such a method.

Hormonal analyses

Fecal sampling

We collected fecal pellets of a vole in the bedding during the pre-test and post-test periods. Because fecal pellets produced in a day reflect the physiological condition of a vole in the previous day (Hume *et al*., 1993; Pei *et al*., 2001), the feces produced on the 1st day post preference test were designated as reflecting the condition on the testing day. Thus, the fecal samples we collected represented three periods: pre-test, preference test, and post-test periods. All fecal samples were stored at -20°C before subjected to the analyses of concentration of steroid hormones, progesterone, estradiol, and corticosterone for females, testosterone and corticosterone for males.

Hormone extraction and EIA

All fecal samples were dried at 40°C for 48 hours and ground into powder. We took 0.1 g of each fecal sample for the subsequent hormone extraction procedures. Each sample was first mixed with 0.8 ml of methanol and 0.1 ml ddH_2O. After shaking (1250 xg) a

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sample for 30 minutes, 0.6 ml petroleum ether was added to each sample. Then, the samples were shaken for another 30 seconds, and centrifuged for 15 minutes at 1600 xg. The solution in the microtube was divided into three layers, from top to bottom, petroleum ether, methanol, and fecal remnant. Next, we transferred 0.6 ml of the hormone-containing methanol layer to a new microtube, and stored it at -20°C until assayed.

The steroid hormone concentrations of the extracted samples were determined with the enzyme-immunoassay (EIA) method. The 0.6 ml samples were diluted using assay buffer, and mixed with steroid hormone-horseradish peroxidase coupler (HRP). Then, the mixed solutions were added to a 96-well plate that was previously coated with the steroid hormone (e.g., progesterone) antibodies. The plate was shaken (100 rpm) for 20–30 minutes. The steroid hormone competed against HRP for antigen-binding sites at room temperature. Then, the plate was washed twice with washing buffer to remove non-binding antigens. Immediately, o-phenylenediamine (OPD) was added to each well, and sit for 20-min color reaction at room temperature. The reaction was stopped by the addition of 8 N sulfuric acid. The absorbency of samples was read with a dual wavelength reader (490/630 nm), and compared with that of the steroid hormone standard curve.

Statistical analyses

We used a paired *t*-test to examine the difference in body weights between adult males and females. The effects of sex (male vs. female) of focal voles and status (partner vs. stranger) of stimulus voles on the four behaviors measured for the focal voles: the choice (prefer-or-not), time in each chamber, time in physical (side-by-side) contact with each vole, and frequency of aggression toward each vole, were analyzed using the following tests. We applied a Fisher's exact test to examine if male and female voles showed differential choice for partner vs. stranger. We used regression analyses to examine if sex or status affected the time spent by focal voles in each chamber and in physical contact with each stimulus voles. The analyses used time as dependent variable, and included sex, status, and sex-by-status interaction as independent variables. Although a vole would act as a focal or stimulus vole in different trials, we were not able to include the identity of vole as a random factor in the analyses due to small sample size. We also calculated the difference in the amount of time spent in the partner chamber versus stranger chamber as a dependent variable, and used *t*-test to examine if males and females were different. We did the same analysis for the amount of time spent in physical contact with each stimulus voles. We used Pearson product-moment correlation analyses to examine the relationship between "time spent in the chamber" and "time spent in physical contact".

We used logistic regression analyses to examine if the choices of focal voles were influenced by steroid hormone concentrations of themselves and stimulus voles, and used regression analyses to examine if the time spent in each chamber and in physical contact with each stimulus voles were influenced by hormone concentrations. We included the average (over 5 days) concentration before pairing, variation (CV over 5 days) of concentration before pairing, and concentration during pairing as the independent variables in separate statistical tests.

RESULTS

Sexual dimorphism in body weight

The adult body weight was 43.19 ± 3.38 g in males and 37.03 ± 3.54 in females. The difference (6.16 ± 3.18 g) was significant (paired *t*-test; $t = 5.47$, $p < 0.001$, Table 1).

Partner preference experiments

Both male and female focal voles tended to spend more time in the partner chamber than in the stranger chamber. Males spent 94.09 ± 16.83 min vs. 74.09 ± 15.98 min in partner and stranger chamber, respectively; and female spent 93.23 ± 12.73 min vs. 54.53 ± 15.39 min in partner and stranger chamber, respectively. Similarly, both male and female focal voles tended to spend more time in physical contact with the partner than the stranger. Males spent 68.11 ± 16.70 min vs. 37.36 ± 15.77 min in physical contact with partner and stranger, respectively (Fig. 1A); and female spent 49.45 ± 14.04 min vs. 27.95 ± 13.21 min in physical contact with partner and stranger, respectively (Fig. 1B). The amount of time spent in the chamber was strongly correlated with the amount of time spent in physical contact for both males and females ($r > 0.77$, $p < 0.02$ in all cases).

We first used the time the focal vole spent in physical contact with the partner vs. stranger to determine choice (i.e., which of the stimulus voles was preferred). Males and females did not show differential preference patterns (Fisher's exact test, $p = 0.38$). Six of the 9 focal males chose their partners, while 6 of the 8 focal females chose their partners. Using the time in each chamber to define preference yielded the same results.

Regression analyses showed that the status of the stimulus voles did not significantly (status effect, $t = -1.47$, $p = 0.15$) affect the amount of time a focal vole spent in physical contact with partner vs. stranger by either male or female focal voles (sex effect, $t = -0.87$, $p = 0.39$; sex-by-status interaction, $t = 0.34$, $p = 0.76$).

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Table 1. Comparisons of body weights (in grams) between males and females of the Taiwan field vole at 90–180 days of age and four other microtine species at 90 days of age. Values in parentheses give the weight difference divided by female weight.

Species	Litters	Body weight (mean ± 1sd)		Weight differences between sexes	p	Reference
		Male	Female	Male−Female		
M. kikuchii	8	43.19 ± 3.38	37.03 ± 3.54	6.16 ± 3.18 (16.6%)	<.001	This study
M. ochrogaster	32	43.5 ± 6.3	37.3 ± 3.8	6.2 (16.6%)	0.001	Dewsbury *et al*. 1980
M. canicaudus	25	31.1 ± 3.9	25.8 ± 3.3	5.3 (20.5%)	0.001	Dewsbury *et al*. 1980
M. pennsylvanicus	25	53.8 ± 6.7	44.2 ± 9.7	9.6 (21.7%)	0.001	Dewsbury *et al*. 1980
M. montanus	25	42.4 ± 5.1	31.4 ± 5.0	11.0 (35.0%)	0.001	Dewsbury *et al*. 1980

Using the amount of time a focal vole spent in each chamber as the dependent variable yielded the same results. Upon examining the difference in the amount of time spent in physical contact with each stimulus voles, there was no significant difference between males and females (*t*-test; $t = 0.25$, $p = 0.81$). Again, using the amount of time a focal vole spent in each chamber as the dependent variable yielded the same results.

We did not observe much aggression between individuals during behavioral trials. The focal females occasionally vocalized to either partners or strangers, but the focal males never did so. Therefore, the aggression was not quantified and analyzed.

Effects of hormones on preference

Steroid hormone concentrations (in terms of any of the three variables) of the partner/stranger voles did not influence the choices of either male or female focal voles (Logistic regression; $p > 0.34$ in all cases; Lee, 2013). Upon examining details, we found steroid hormone concentrations of the partner/stranger voles did not influence the time spent in a chamber nor the time spent in physical contact with a stimulus vole by either male or female focal voles (Linear regression; $p > 0.16$ in all cases; Lee, 2013).

DISCUSSION

1. Sexual dimorphism

The body weight of adult male Taiwan field voles was significantly greater than that of females (Table 1). Clearly, there is body weight dimorphism. A review by Dewsbury *et al*. (1980) found that males were significantly heavier than females in 10 of the 13 muroid rodents at 90 days of age. For the 3 species with no sexual dimorphism: *Peromyscus polionotus, Onychomys leucogaster*, and *Peromyscus eremicus,* evidence exist suggesting they are monogamous. All four Taiwan field vole congeners: prairie vole (*M. ochrogaster*), gray-tailed vole (*M. canicaudus*), meadow vole (*M. pennsylvanicus*) and montane vole (*M. montanus*) reported in Dewsbury *et al*. (1980, Table 1) showed sexual dimorphism in body weight with males heavier than females. The difference in the Taiwan field vole was 6.16 g, or a 16.6% difference, which was similar to that of prairie voles (16.6%), a species considered monogamous. The value was lower than the other 3 species (20.5–35.0%), all considered polygynous or promiscuous (Madison, 1980; Dewsbury, 1981; McGuire and Novak, 1986; Boonstra *et al*., 1993; Wolff *et al*., 1994). Although the Taiwan field vole had significant sexual dimorphism, the interspecific comparison (Table 1) provided support for a monogamy mating system.

2. Partner preferences

The results of our partner preference tests indicated that Taiwan field voles did not have significant preference for the cohabitation partner (Fig. 1). The male and female partners did not form pair bonds. What does such a result mean? There are three potential explanations: (1) The result is inconclusive, because sample size is small. (2) The result is inconclusive, because cohabitation is too short. (3) The result indicates that Taiwan field vole mating system may not be monogamy. In response to explanation 1, we admit

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the sample sizes were indeed small. Although the focal vole showed a slight preference in spending more time in partner chamber or in physical contact with partner than stranger, the trend was very weak (Fig. 1). Increasing sample sizes would have little help in strengthening the differences. In response to explanation 2, there is no empirical study available that indicates the length of cohabitation required for examining partner preference. The only related study (Williams *et al*., 1992) we know of indicated that 24-hr cohabitation is sufficient to generate the preference for partner in prairie voles. Prairie vole is a "model" monogamous species. Its mating system has been examined in the field and laboratory in numerous studies (Thomas and Birney, 1979; Getz *et al*., 1981; Carter *et al*., 1995). We argue that the use of 24-hr cohabitation, a conservative design, should be employed in the partner preference test. Our notion was that if Taiwan field voles were as monogamous as prairie voles, we should be able to see strong partner preference in both males and females (Williams *et al*., 1992) even with small sample sizes. However, we did not. Finally, we should consider the possibility that the mating system of Taiwan field voles may not be strictly monogamy because male and female partners do not form pair bonds.

Less than 3% of mammalian species examined show monogamy (Kleiman, 1977; Wittenberger and Tilson, 1980; Carter and Getz, 1993). Compared to other taxonomic groups, mammalian females have to stay with young due to pregnancy and milk-nursing, which gives males the opportunity to mate with other females. Thus, it takes unique environmental situation for monogamy to occur in mammals. Monogamy may occur only when there is little opportunity for being polygamous (Wittenberger and Tilson, 1980). For example, when male parental care is necessary for female reproductive success, or when an individual has less fitness with two or more mates than with one, the mating system is likely to show a "monogamy pattern" (Wittenberger and Tilson, 1980).

Do field situations push the Taiwan field vole toward a monogamous mating pattern? Nearly all field studies on the ecology of Taiwan field voles came from populations in a Yushan cane grassland in the He-huan Mountain. In such a habitat, one of us (LKL) and colleagues (Wu, 1998; Chen *et al*., 2006; Wu *et al*., 2012) have found supports for a monogamy mating system in previous studies. As discussed earlier in the introduction, we consider the available information insufficient to establish the Taiwan field vole as a monogamous species. Although our sexual dimorphism result lent support to monogamy, the partner preference results did not. Three additional studies suggested the mating system may be flexible. Quan *et al*. (2010) in a 6-week daily trapping study found home range overlaps among multiple adult males and females, and clearly illustrated a non-monogamy pattern during breeding season (June and July). Although it was a study in the alpine forest habitat, the results suggested that the mating system of Taiwan field voles is likely habitat-dependent. Second, Liang (2012) showed that trapping at nest sites often capture more than a pair of adults, particularly during early breeding season (March–June). It suggested that the mating system of Taiwan field voles is likely season-dependent. Finally, Chappell *et al*. (in review) found that the density of receptors for OTR binding in the nucleus accumbens, a positive indication of pair bonding, was low in Taiwan field voles. The level was between those of prairie voles (a monogamous species) and meadow voles (a promiscuous species). Based on the

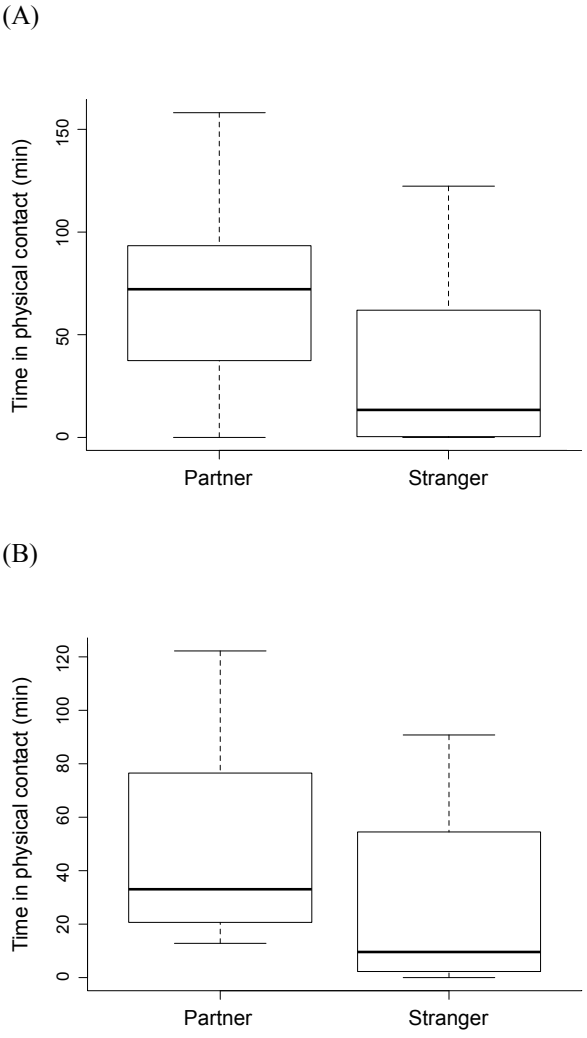


Fig. 1. The amount of time a focal vole spent in physical contact with partner vs. stranger by (A) male or (B) female focal voles.

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evidence from this and other studies, we propose that the mating system of the Taiwan field vole is not strictly monogamy, but flexible.

Indeed, many ecological factors, such as resource availability and dispersion, mate availability and dispersion, and predation risk may affect mating system (Orians, 1969; Kleiman, 1977; Emlen and Oring, 1977; Wittenberger and Tilson, 1980). Many studies have indicated that the mating system of the same species can be different in response to varied situations, such as habitat quality, seasonality, and population density (Getz *et al*., 1987; McGuire *et al*., 1993; Cushing *et al*., 2001; Parker *et al*., 2001). The mating system of a species may display intraspecific variations in response to different environmental conditions (Lott, 1984). For example, prairie voles displayed a polygamous mating system during winter breeding season and under high population densities in east-central Illinois (Getz *et al*., 1987; McGuire *et al*., 1993). The species showed year round polygyny in the more xeric habitat of eastern Kansas (Fitch, 1957; Gaines and Johnson, 1984; Swihart and Slade, 1989). In contrast, promiscuous meadow voles may develop monogamous-like behaviors: selective partner preference and stranger- directed aggression during the colder months of the year or under low population density during the summer breeding season (Madison *et al*., 1984; Parker *et al*., 2001). Similarly, the mating system of the Taiwan field vole likely depends on environmental conditions. Certain ecological conditions in the forest habitat (Quan *et al*., 2010) or early breeding season (Liang, 2012) may drive the mating system away from monogamy. In this study, all experimental voles were housed in the breeding room. They did not suffer stresses from food, weather and predators. Monogamy might not be necessary for voles living under such a condition.

3. Steroid hormones

We did not find gonadal hormone concentrations affect the outcomes of the partner preference tests of the Taiwan field vole. It conformed to the previous studies shown for the prairie vole (Williams *et al*., 1992; DeVries *et al*., 1997). Partner preference in female prairie voles could be established after a 24 hr-cohabitation, and would not be enhanced further by mating or longer cohabitation periods (48 hr, Williams *et al*., 1992). In both sexes, preferences were not influenced by the presence or absence of gonadal hormones (DeVries *et al*., 1997). On the other hand, we did not find effect of corticosterone on partner preference in the Taiwan field vole. It did not conform to the previous studies shown for the prairie vole (DeVries *et al*., 1995; 1996; Carter *et al*., 1997). The hormone was shown to have a sex-dependent effect on prairie voles. Exposure to the stress of swimming or injections of corticosterone facilitated the development of partner preference in males, but not females. Many studies indicated that the neuropeptides oxytocin and vasopressin could facilitate pair bonding and partner preference in female and male prairie voles, respectively (Winslow *et al*., 1993; Williams *et al*., 1994; Insel and Hulihan, 1995). Stress or corticosterone treatments might release vasopressin directly or indirectly through neurochemical mechanisms and facilitated preference in males. In females, these treatments might inhibit preference because they interfered with the release or action of oxytocin. It is possible that the non-significant effects of corticosterone in our study were due to the use of a different methodology. In previous studies, the corticosterone treatments were removal of the adrenal gland or addition of artificial doses. We used natural fecal corticosterone concentration in this study. The range of natural variations in corticosterone concentration might not be enough to reveal the effects on pair bonding and resulting partner preferences.

4. Conclusions

Taiwan field voles showed little sexual dimorphism, and fulfilled a monogamy syndrome (item 1). However, the species did not exhibit significant partner preference, and failed to meet a critical monogamy syndrome (item 2)—long-term pair bonding. It suggests that mating system of the Taiwan field vole may not be strictly monogamy. Considering evidence from recent studies (Quan *et al*., 2010; Liang, 2012; Chappell *et al*., in review), we think that the mating system of the Taiwan field vole is likely flexible, and call for further studies. Several other monogamy syndromes (items 6 and 7) have yet to be examined in *M. kukuchii*. Particularly, future studies should investigate if the species show incest avoidance and reproductive suppression by adult individuals within a family; if social factors regulate reproductive physiology (e.g., estrus induction and ovulation).

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從伴侶偏好看台灣高山田鼠的婚配制度

李佳倩[1]、邱智賢[2]、林良恭[3]、林雨德[1,4*]

1. 國立台灣大學生態學與演化生物學研究所，台北市羅斯福路四段 1 號，10617。
2. 國立台灣大學動物科學技術學系，台北市羅斯福路四段 1 號，10617。
3. 東海大學生命科學系，台中市西屯區臺灣大道四段 1727 號，40704。
4. 國立台灣大學生命科學系，台北市羅斯福路四段 1 號，10617。
* 通信作者。*Tel.: 02-33664534; Email: kirklin@ntu.edu.tw*

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摘要：台灣高山田鼠 (*Microtus kikuchii*) 的婚配制度極可能是哺乳類中罕見的一夫一妻制。一夫一妻制動物會表現伴侶偏好行為，即行為上偏好同居或配對過的異性個體顯著多於陌生個體，但伴侶偏好可能會受到固醇類賀爾蒙(性賀爾蒙及壓力賀爾蒙) 濃度左右。我們以伴侶偏好行為實驗 (partner preference test) 測試台灣高山田鼠是否表現 [同居過的雌雄個體接觸時間應顯著多於與陌生個體的接觸時間]，過程以錄影記錄並進行分析。另一方面，在行為實驗的前及後4–5天收集高山田鼠每日的糞便，以酵素免疫分析法 (enzyme-immunoassay method) 獲得實驗雄性田鼠的睾固酮 (testosterone)、雌性田鼠的孕酮 (progesterone) 和雌二醇 (estradiol) 及每隻田鼠的壓力賀爾蒙 (corticosterone)。伴侶偏好行為實驗結果顯示雌性與雄性高山田鼠均沒有任何伴侶偏好。在實驗前後的固醇類賀爾蒙濃度亦未顯示對高山田鼠個體的伴侶偏好有任何顯著性的影響。另一方面，高山田鼠具有較小的體重雌雄二型性，與一夫一妻制的草原田鼠 (*M. ochrogaster*) 相似。由於台灣高山田鼠並未表現出伴侶偏好行為，其婚配制度可能不是嚴謹的一夫一妻制。未來其婚配制度的研究需檢視更多與一夫一妻制相關的生理現象，並探討婚配制度可能依環境而易的情況。

關鍵詞：酵素免疫分析法、婚配制度、伴侶偏好行為實驗、固醇類賀爾蒙、雌雄二型性、台灣高山田鼠。

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