POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	56	4	701–708	2008

Regular research paper

Ping SUN[1, 2, 3], Wenyan ZHU[1], Xinquan ZHAO[2]

[1] Henan University of Science and Technology, Luoyang 471003, China, e-mail: pingsunny@msn.com;
[2] Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining, 810001, China;
[3] Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101

OPPOSITE-SEX SIBLING RECOGNITION IN ADULT ROOT VOLE, *MICROTUS OECONOMUS* PALLAS: PHENOTYPE MATCHING OR ASSOCIATION

ABSTRACT: Hypothesis of phenotype matching and association are the most likely mechanisms in kin recognition. These hypotheses were tested by observing behavioral responses of cross-fostered root voles to urine cues from familiar and unfamiliar kin and non-kin. In experiment I, approach latency by males was significantly longer in response to non-sibling reared together (NSRT) than to non-sibling reared apart (NSRA) females, whereas, investigatory and sniffing time were significantly less in response to NSRT than to NSRA. However females showed no event bias to odors from NSRT and NSRA males. In experiment II, the behavioral responses of males and females to urine odors from siblings reared apart (SRA) and NSRA were not related to the degree of genetic relationship. It was concluded that: Association mechanism is used by male root voles in opposite-sex sibling recognition; Female voles possibly adopt multiple recognition mechanisms in different social tests.

KEY WORDS: root vole (*Microtus oeconomus* Pallas), kin recognition, phenotype match, association

1. INTRODUCTION

Kin recognition is important in many aspects of social behavior in mammals (Hepper 1991, Todrank *et al.* 1998, Mateo and Johnston 2000a, Tai *et al.* 2000, 2002, Zhang *et al.* 2002, Mateo 2002, Johnston 2003). Mechanisms for kin recognition by odor cues have been widely investigated and reviewed (Holmes and Sherman 1983, Sherman and Holmes 1985, Waldman 1987, Blaustein and Porter 1990, Halpin 1991, Hepper 1991, Mateo and Johnston 2000b, Mateo 2003, 2004). Two most likely mechanisms for kin recognition were accepted by most scientists: phenotype matching, that is, classifying individuals as kin because they share family characteristics (see overview Mateo 2003, 2004); and recognition by association, i.e. animals learn the phenotypes of individuals during early development (e.g., siblings and parents) and later discriminate these familiar relatives from unfamiliar animals (Porter 1986, Halpin 1991). There is a great number of evidences to support both recognition mechanisms in a variety of rodent species including house mice, *Mus musculus* (L) (Kareem and Barnard 1982), Belding's ground squirrels, *Spermophilus beldingi* Merriam (Holmes and Sherman 1982, 1983, Holmes 1986a, b, Mateo and Johnston 2000a, Mateo 2003), spiny mice, *Acomys cahirinus* Desmarest (Porter 1986), golden-mantled ground squirrels, *S. lateralis*

Say (Holmes 1995, Mateo 2002), beaver, *Castor canadensis* Kuhl (Sun and Müller-Schwarze 1997), and golden hamsters, *Mesocricetus auratus* Waterhouse (Mateo and Johnston 2000b, 2003). In addition, there is an interesting founding which does not support the mechanism of phenotype matching (van der Jeugd *et al.* 2002).

Despite considerable research on these issues, there are still many questions remaining about how kin recognition is achieved. One question is whether recognition by association and by phenotype matching are distinct mechanisms or whether there is sufficient overlap in the two processes that they should be considered different aspects of the same basic mechanism (Heth *et al.* 1998, Mateo 2004), that is, is there concurrent effect in kin recognition? Individuals could learn individual cues from their littermates (and possibly cues from self or parents) and use these cues as the basis for developing a family template for recognition of both familiar and unfamiliar kin (Waldman 1987, Waldman *et al.* 1988, Blaustein and Porter 1990, Mateo and Johnston 2000b). Alternatively, individuals could learn the cues from individual littermates and remember them as individuals but not generalize from these cues to those of other relatives (Halpin and Hoffman 1987, Halpin 1991). Another important question concerns whether sexual difference results in different mechanisms for kin recognition during different developmental periods.

However, under controlled conditions, the ability and the mechanism of root voles to recognize kin for extended periods have not been examined yet. Production and perception of recognition cues in *Microtus* could help us understand whether it can discriminate between kin and non-kin, familiar and unfamiliar, or which mechanism root vole would adopt.

Based on this knowledge, one would expect whether root voles could discriminate odors from kin and non-kin. And also whether male and female voles adopt the same mechanism for kin recognition. If yes, which mechanism would be adopted by them; if no, which mechanism will be adopted by male and females respectively and why? In response to odors from sibling, one would expect less interesting in opposite-sex kin because of incest avoidance, however, in response to odors from non-sibling, one would expect more interest in soliciting non-kin as mates to increase genetic variability. To determine whether root voles respond differentially depending on their degree of genetic relationship to the odor donors (which would be evidence to support phenotype matching mechanism) or on their familiarity with the odor donors (which would be further evidence for the recognition-by-association mechanism), the behavioral responses to urine odors from familiar and unfamiliar sibling and non-sibling were investigated by behavioral choice maze.

2. MATERIALS AND METHODS

2.1. Study animals

Adult root voles (80 days old) were third generation offspring of field-caught animals born and raised under a long day photoperiod (14:10 h light: dark cycle, lights on at 08:00 and end at 22:00 hours 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 22±2 °C (Zhuo Yi Electron Ltd.). Food and water were provided *ad libitum*. Once a week, cages were cleaned and cotton-nesting material was replaced. All animals were used only once in a month to avoid the effect of repeated utilization.

2.2. Cross-foster experiment

Multiple-transfer design was used in cross-foster experiment (Mateo and Holmes 2004). Firstly, 2 litters of pups were chosen. Their parents were shut away by cages before pups were separated from their parents. Then 2 pups from one litter and an equal number from another litter were exchanged reciprocally shortly after birth. Next, the pups were wiped clean with water-soaked cotton balls and dipped in sawdust containing urine and feces of their foster parents for 5 min. Then the parents were freed. To avoid the infanticide, the pubs would be taken away once they suffered aggression from their foster parents.

To reduce the possible effects of cross-fostering, litter size and sex ratio were unchanged for the two fostered groups in each. Latex gloves were worn when handling pups.

Fostered vole pups were housed with their foster parents in the clear polycarbonate cages until separation from their parents on day 20 after birth (Liang *et al.* 1982). After weaning, cross-fostered animals were housed in standard cages containing groups of two to four animals and treatment conditions.

So, there were three kinds of litters including non-sibling reared together (NSRT), non-sibling reared apart (NSRA), and sibling reared apart (SRA).

2.3. Experimental equipment

The behavioral choice maze included one odorant box (30×30×30 cm) and one neutral box (30×30×30 cm) which were made of organic glass. Odorant box and neutral box were connected by pellucidly organic glass tube (20 cm in long and 7 cm in diameter). The culture dish contained the fresh urine was put in the central of odorant boxes as stimulant. There was a switch between odorant and neutral boxes that controlled the passing in and out of experimental voles.

2.4. Experimental procedure

The odor donors (stimulus voles) were captured in the hutch and put on the clear cages. There were two layers of gauze to segregate feces and urine. The fresh urine (aged less than 20 min) sucked by absorbent cotton was put in the culture dish as the stimulus.

All behavioral observations were conducted in a separate colony room that had the same conditions in temperature, light and aeration. All tests persisted 10 min and were carried out during the light phase, between 09:00 and 18:00 h. Experimental animal habituated in behavioral choice cages and 5 min later it was fixed by transparent tube at the central of neutral box. Then the odorants were put in the central of odorant box. Two minutes later the strobe was opened, subject was set free and the behavior of voles was recorded.

Urine from NSRT, NSRA, and SRA was used as the stimulus odor. The strange odor donors were of similar body weight and age to experimental animals and generally they were used only once in this experiment. Subjects and strange donors for the experiment were kept in isolation before testing. So subjects had never met the strange donors and the effect of previous contests could be excluded.

2.5. Experimental design

Two separate protocols were conducted.

Experiment I: Can root voles discriminate the odors from familiar and unfamiliar opposite-sex non-kin?

In this experiment we investigated whether subjects would discriminate between the urine odors of unrelated conspecifics, which were familiar and unfamiliar to the subject, to determine the importance of association experience with scent donors for discrimination.

40 voles (including 20 males and 20 females) were used in this experiment. They were divided into 2 groups. One group was designed to examine the behavioral responses of males to odors from NSRA and NSRT females. Another one was designed to examine the behavioral responses of females to urine cues from NSRA and NSRT males.

Experiment II: Can root voles show significant preference to the odors from genetically related opposite-sex unfamiliar kin or non-kin?

In experiment 1, no matter male and female voles show the same or different behavioral responses to odors from familiar and unfamiliar objects of opposite-sex. It helps us to understand the effect of the familiarity of nestmates compared to strangers on kin recognition, it is not clear from these results, and however, the differences in behavioral responses were not due to the genetic relationship of the siblings. This study was designed to determine whether there is genetic recognition between the voles and their socially unknown biological opposite-sex siblings (SRA). The control animals (NSRA) were chosen at same age as SRA.

40 voles (including 20 males and 20 females) were used in this experiment. They were divided into 2 groups. One group was designed to examine the behavioral responses

of males to odors from SRA and NSRA females. Another one was designed to examine the behavioral responses of females to urine cues from SRA and NSRA males.

2.6. Data collection and analysis

The experimental voles' behavior was recorded for 10 min. The approach latencies (AP) to leave the neutral to odorant box and the time spent in odorant boxes (investigatory time, IT) were measured. During all tests we timed how long the tested root voles spent sniffed the stimulus odorants (that is, brought their nostrils to within ca. 0.5 cm of the stimulus, apparently sniffing, ST). Before being used next time, behavioral choice cases were cleaned out with a 75% alcohol solution, washed by clear water and air-dried then.

If experimental animals did not leave the neutral to odorant box within 5 min, and/or it stayed in the tube exceeded for 3 min, the test would be terminated.

Behavioral data were compared by Mann-Whitney test for dependent samples. All differences were regarded as statistically significant at $P < 0.05$.

3. RESULTS

Mann-Whitney test (calculated using SPSS 11.0) indicated that male root voles exhibited different behavioral responses in respond to odors from familiar and unfamiliar non-siblings. Male voles entered the unfamiliar odorant box significantly earlier than the familiar one (Fig. 1, left: $Z = -2.075$, $P < 0.05$). Males spent more time in visiting strange non-sibling than familiar one (Fig. 1, middle: $Z = -1.987$, $P < 0.05$). There was significant difference in the mean ST in response to odors from familiar and unfamiliar non-sibling in males (Fig. 1, right: $Z = -2.340$, $P < 0.05$).

Otherwise, females showed no evident bias to familiar and unfamiliar unrelated odors (Fig. 2, left: $Z = -1.777$, $P > 0.05$). The difference of IT to familiar and unfamiliar non-sibling by females was non-significant (Fig. 2, middle: $Z = -1.510$, $P > 0.05$). There was insignificant difference of ST in response to familiar and unfamiliar non-sibling's odors in females, too (Fig. 2, right: $Z = -1.688$, $P > 0.05$).

Male root voles showed no evident preference to odors from unfamiliar sibling (SRA) and non-sibling (NSRA) (Table 1). There

Table 1. Behavioral responses to females of siblings and non-siblings reared apart by male voles (mean ± SE).

Behavioral Variable	Siblings reared apart (10)	Non-siblings reared apart (10)	Z - Value	*P* - Value
Approach Latency (s 10 min^{-1})	16.54 ± 6.17	40.33 ± 24.32	0.000	1.000
Investigatory Time (s 10 min^{-1})	443.31 ± 33.10	402.96 ± 27.51	−0.866	0.386
Sniff/lick Time (s 10 min^{-1})	51.04 ± 26.84	34.71 ± 11.86	0.000	1.000

Mann-Whitney U-test. The number in the bracket indicates the sample size.

Table 2. Behavioral responses to males of siblings and non-siblings reared apart by female voles (mean ± SE).

Behavioral Variable	Sibling reared apart (10)	Non-sibling reared apart (10)	Z - Value	*P* - Value
Approach Latency (s 10 min^{-1})	55.18 ± 20.33	67.59 ± 13.55	−0.889	0.374
Investigatory Time (s 10 min^{-1})	426.11 ± 34.51	382.87 ± 29.20	−1.066	0.286
Sniff/lick Time (s 10 min^{-1})	48.28 ± 14.13	28.11 ± 7.21	−1.066	0.286

Mann-Whitney U-test. The number in the bracket indicates the sample size.

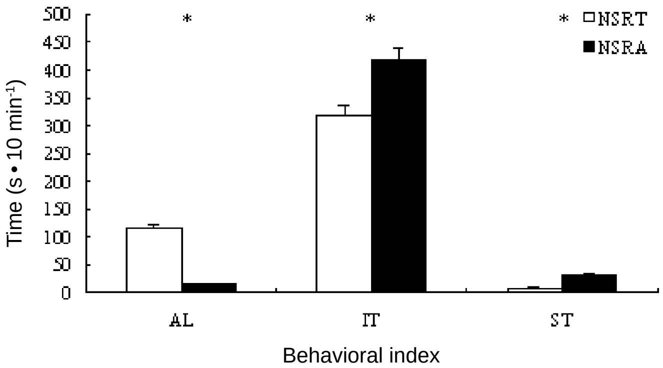

Fig. 1. Behavioral responses of male voles to females of non-sibling reared apart (NSRA) and non-sibling reared together (NSRT). AL: Approach latency; IT: Investigatory time; ST: Sniff time. *: $P < 0.05$.

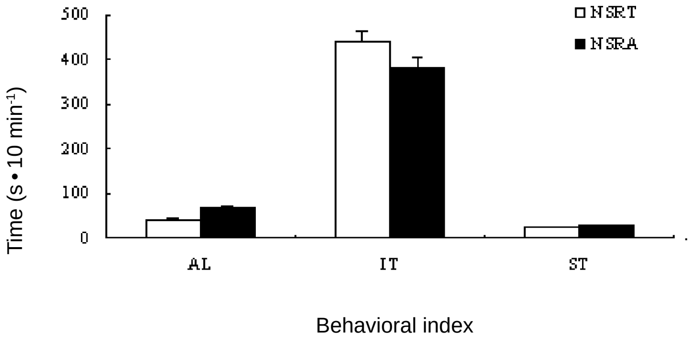

Fig. 2. Behavioral responses of female voles to males of non-sibling reared apart (NSRA) and non-sibling reared together (NSRT). AL: Approach latency; IT: Investigatory time; ST: Sniff time.

were insignificant differences between SRA and NSRA in AL (Z = 0.000, *P* = 1.000), IT (Z = – 0.866, *P* = 0.386), and VT (Z = 0.000, *P* = 1.000) in male voles.

Females also could not discriminate the odors from SRA and NSRA (Table 2). There was no difference in AL to unfamiliar siblings and non-siblings in females (Z = –0.889, *P* = 0.374). At the same time, there were insignificant differences in the mean of IT (Z = –1.066, *P* = 0.286) and ST (Z = –1.066, *P* = 0.286) towards SRA and NSRA, separately.

4. DISCUSSION

In experiment I, males and females showed different behavioral responses to odors from familiar and unfamiliar opposite-sex non-siblings (Figs 1, 2). The different behavioral responses of males to NSRA and NSRT suggest that familiarity had significant effect on males' kin recognition, in other words – males used an association mechanism to estimate odors from familiar and unfamiliar opposite-sex non-kin. The similar behavioral responses of females to NSRA and NSRT suggest that female voles could not discriminate between familiar and unfamiliar opposite-sex non-siblings, i.e. females adopt phenotype matching in recognizing familiar and unfamiliar opposite- sex non-kin urine cues. In addition, in experiment II, males and females showed similar behavioral responses to odors from SRA and NSRA (Tables 1, 2). The results suggest that the degree of genetic relationship to odor donors had no influence on their responses, so root voles used an association mechanism to evaluate odors from unfamiliar kin and non-kin. In conclusions, male root voles adopted association mechanism in discrimination familiar and unfamiliar kin and non-kin; females applied phenotype-matching and association mechanisms synthetically in recognizing familiar and unfamiliar kin and non-kin.

4.1. Familiarity and sibling recognition

Some results suggest the importance of social experience in sibling discrimination. Both meadow and prairie voles recognize siblings on the basis of familiarity, rather than on genetic relationship per se (Ferkin and Rutka 1990, Ferkin *et al.* 1992, Paz y Miño and Tang-Martinez 1999). In addition, Holmes (1986b) found that female Belding's ground squirrels were less aggressive towards the sisters of their foster-siblings than towards other unfamiliar, unrelated females and suggested that this difference was due to indirect familiarity. In the experiments reported here with male root voles (not females), behavioral responses depended on the degree of familiarity rather than genetic relationship through common cross-fostering.

Voles disperse shortly after weaning (Boonstra *et al.* 1987, Ims 1990). Some disperse short distances and establish themselves in the neighborhood of the natal area (i.e. within the maternal home range, Lambin *et al.* 1992), and others disperse over several kilometers (Liro and Szacki 1987, Steen 1994). Otherwise, females will stay with their mother (Lambin *et al.* 1992, Andreassen *et al.* 1998, Bjornstad *et al.* 1998). In spite of shortage of the data which can indicate the disperse patterns of root voles, our data suggested that male root voles distributed in Qinghai-Tibet plateau may disperse about 60 ~ 70 m. The remembrance of the odors from the opposite-sex siblings will be unnecessary to inbreeding avoidance. This will explain our results why male voles adopt association in sibling recognition.

4.2. Genetic relationship and sibling recognition

Recognition by phenotype matching involved comparing conspecific odors with their own odor (or a kinship odor learned in the first week of life) and classifying (and responding to) these conspecific odors based on their degree of similarity to the odor template. Kareem and Barnard (1982) found that when the subjects were familiar with each other the effects of relationship disappeared. Holmes and Sherman (1982) found that Belding's ground squirrel juveniles and adults could use phenotype matching to discriminate among unfamiliar individuals based on genetic relationship (Holmes 1986a, b, Mateo 2002).

4.3. Concurrent effect and sibling recognition

Species can use multiple different recognition mechanisms in different social contexts, and during their lifetimes the perceptual component changes and needs to be continually updated (Mateo 2004). In addition, Tang-Martinez (2001) suggested that prior association and phenotype matching are involved in all recognition situations, i.e. concurrent effects. Belding's ground squirrel mothers utilize spatial cues to recognize among young, caring any pups in their underground nest. After weaning, mothers can use a prior-association mechanism for discriminating own and unfamiliar young (Holmes and Sherman 1982). *S. beldingi* can also use phenotype matching to recognize unfamiliar relatives of non-kin (Mateo 2002) and can use prior association to discriminate among individual non-kin (Mateo 2004). Golden hamster has at least two kinds of kin recognition mechanisms: familiarity (established during early rearing) and self-referent phenotype matching (Mateo and Johnston 2000b). In our experiment, female root voles adopt different recognition mechanisms in different socially discriminating experiments.

The relative importance of kinship and familiarity in the different treatment of kin has been studied by a number of investigators and the results have varied across species. In mice, Kareem and Barnard (1982) found that difference in aggressiveness towards full- and half- siblings were due to differences in familiarity and that difference in aggressiveness towards unfamiliar half-siblings and non-siblings were due to phenotype matching. In juvenile golden mantled ground squirrels, effects of both familiarity and genetic relationship have been found;

individuals play most with familiar siblings and least with unfamiliar non-siblings, but they play more with foster-siblings than unfamiliar siblings (Holmes 1995). Porter (1986) concluded that in spiny mice, phenotype matching is less effective than familiarity for sibling recognition.

In nature, some abilities working together have two main helps: optimizing outbreeding through appropriate mate selection and increasing inclusive fitness (Hamilton 1964) through preferential treatment of genetic relatives (nepotism). These abilities include that recognizing individual littermates from their odors and comparing odors from unfamiliar conspecifics with one's own odor to judge relationship. Unfortunately, very little is known about the behavioral ecology of root voles, and it is difficult to evaluate realistically how these different recognition mechanisms function in nature. Like many sociality rodents, root voles' home ranges were overlapped or adjacent to those of other individuals (Sun *et al.* 1982). Some of these neighbors may be former nestmates, familiar or unfamiliar half-siblings or other kin, or unknown nonkin, and it would be valuable to know how these separate recognition mechanisms (recognition of familiar nestmates and kin recognition based on phenotype matching) influence their social interactions.

ACKNOWLEDGEMENTS: This research was supported by the grant from Natural Science Foundation grant 30500073, 30870370 and China Postdoctoral Foundation 20070420525 to P. Sun. We thank Meiling Zhang for help in caring for our colony of root voles. This research performed with the permission of the Ethical committee for animal experiments in Qinghai province, China.

5. REFERENCES

Andreassen H.P., Hertzberg K., Ims R.A. 1998 – Space use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus* – Ecology 79: 1223–1235.

Blaustein AR., Porter R.H. 1990 – The ubiquitous concept of recognition with special reference to kin. (In: Interpretation and Explanation in the Study of Animal Behavior, Vol. I: Interpretation, Intentionality and Communication Eds: Bekoff M. Jamieson D.) – Westview Press, Boulder, Colorado, 123–148.

Bjornstad O.N., Andreassen H.P., Ims R.A. 1998 – Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus* – J. Anim. Ecol. 67: 127–140.

Boonstra R., Krebs C.J., Gaines M.S., Johnson M.L., Craine, I.T.M. 1987 – Natal philopatry and breeding systems in voles (*Microtus spp.*) – J. Anim. Ecol. 56: 655–673.

Ferkin M.H., Rutka T.F. 1990 – Mechanisms of sibling recognition in the meadow vole – Can. J. Zool. 68: 609–613.

Ferkin M.H., Tamarin R.H., Pugh S.R. 1992 – Cryptic relatedness and the opportunity for kin recognition in microtine rodents – Oikos, 63: 328–332.

Halpin Z.T. 1991 – Kin recognition cues in vertebrates. (In: Kin Recognition, Ed. P. Hepper) – Cambridge University Press, Cambridge 220–258.

Halpin Z.T., Hoffman M.D. 1987 – Sibling recognition in white-footed mouse, *Peromyscus leucopus*: association or phenotype matching – Anim. Behav. 35: 563–570.

Hamilton W.D. 1964 – The genetic evolution of social behavior, I, II – J. Theor. Biol. 7: 1–52.

Hepper P.G. (Ed.) 1991 – Kin Recognition – Cambridge University Press, Cambridge.

Heth G., Todrank J., Johnston R.E. 1998 – Kin recognition in golden hamsters: evidence for phenotype matching – Anim. Behav. 56: 409–417.

Holmes W.G. 1986a – Identification of parental half-sibling by captive Belding' ground squirrels – Anim. Behav. 34: 321–327.

Holmes W.G. 1986b – Kin recognition by phenotype matching in female Belding' ground squirrels – Anim. Behav. 34: 38–47.

Holmes W.G. 1995 – The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: effects of rearing and relatedness – Anim. Behav. 50: 309–322.

Holmes W.G., Sherman P.W. 1982 – The ontogeny of kin recognition in two species of ground squirrels – Am. Zool. 22: 491–517.

Holmes W.G., Sherman P.W. 1983 – Kin recognition in animals – Am. Sci. 71: 46–55.

Ims R.A. 1990 – Determinants of natal dispersal and space use in the grey-sided vole, Clethrionomys rufocanus: a combined laboratory and field experiment – Oikos, 57: 106–113.

Johnston R.E. 2003 – Chemical communication in rodents: from pheromones to individual recognition – J. Mammal. 84(4): 1141–1162.

Kareem A.M., Barnard C.J. 1982 – The importance of kinship and familiarity in social interactions between mice – Anim. Behav. 30: 594–601.

Lambin X., Krebs C.J., Scott B. 1992 – Spacing system of the tundra vole *Microtus oeconomus* during the breeding season in Canada's western Arctic – Can. J. Zool. 70: 2068–2072.

Liang J.R., Zeng J.X., Wang Z.W., Han Y.C. 1982 – The growth and development of root vole (*Microtus oeconomus*) – Plateau Biol. Sin. 1: 195–207. (in Chinese with English summary)

Liro A., Szacki J. 1987 – Movement of field mouse *Apodemus agrarius* (Pallas) in a suburban mosaic of habitats – Oecologia, 74: 438–440.

Mateo J.M. 2002 – Kin-recognition abilities and nepotism as a function of sociality – Proc. R. Soc. Lond. B. 269: 721–727.

Mateo J.M. 2003 – Kin recognition in Ground squirrels and other rodents – J. Mammal. 84(4): 1163–1181.

Mateo J.M. 2004 – Recognition systems and biological organization: the perception component of social recognition – Ann. Zool. Fenn. 41: 729–745.

Mateo J.M., Holmes W.G. 2004 – Cross-fostering as a means to study kin recognition – Anim. Behav. 68: 1451–1459.

Mateo J.M., Johnston R.E. 2000a – Retention of social recognition after hibernation in Belding's ground squirrels – Anim. Behav. 59: 491–499.

Mateo J.M., Johnston R.E. 2000b – Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching – Proc. R. Soc. Lond. B. 267: 695–700.

Mateo J.M., Johnston R.E. 2003 – Kin recognition by self-referent phenotype matching: weighing the evidence – Anim. Cogn. 6: 73–76.

Paz y Miño C.G., Tang-Martinez Z. 1999 – Social interactions, cross-fostering, and sibling recognition in prairie voles (*Microtus ochrogaster*) – Can. J. Zool. 77: 1631–1636.

Porter R.H. 1986 – Chemical signals and kin recognition in spiny mice (*Acomys cahirinus*). (In: Chemical Signals in Vertebrates, Eds: D. Duvall, D. Muller-Schwarze, R.M. Silverstein) – Plenum, New York, Vol. 4: 397–411.

Sherman P.W., Holmes W.G. 1985– Kin recognition: issues and evidence. (In: Experimental Behavioral ecology and sociobiology Eds: B. Holldobler, M. Lindauer) – G. Fischer Verlag, Stuttgart, 437–460.

Steen H. 1994 – Low survival of long distance dispersers of the root vole (*Microtus oeconomus*) – Ann. Zool. Fenn. 31: 271–274.

Sun L., Müller-Schwarze D. 1997 – Sibling recognition in the beaver: a field test for phenotype matching – Anim. Behav. 54: 493–502.

Sun R.Y., Zheng S.W., Cui R.X. 1982 – Home range of the root vole, *Microtus oeconomus* – Acta Theriol. Sin. 2 (2): 219–232. (in Chinese with English summary)

Tai F., Sun R., Wang T. 2002 – Does low fecundity reflect kin recognition and inbreeding avoidance in the mandarin vole (*Microtus mandarinus*) – Can. J. Zool. 80: 2150–2155.

Tai F., Wang T., Zhao Y. 2000 – Inbreeding avoidance and mate choice in the mandarin vole (*Microtus mandarinus*) – Can. J. Zool. 78: 2119–2125.

Tang-Martinez Z. 2001 – The mechanism of kin discrimination and the evolution of kin recognition in vertebrates: A critical re-evolution – Behav. Process. 53: 21–40.

Todrank J., Heth G., Johnston R.E. 1998 – Kin recognition in golden hamsters: evidence for kinship odours – Anim. Behav. 55: 377–386.

van der Jeugd H.P., van der Veen I.T., Larssond K. 2002 – Kin clustering in barnacle geese: familiarity or phenotype matching – Behav. Ecol. 13(6): 786–790.

Waldman B. 1987 – Mechanisms of kin recognition – J. Theor. Biol. 128: 159–185.

Waldman B., Frumhoff P.C., Sherman P.W. 1988 – Problems of kin recognition – Trends in Ecology and Evolution, 3: 8–13.

Zhang L., Sun R.Y., Fang J.M. 2002 – Odor preferences of adult male brandt's vole (*Microtus brandti*) – discrimination of female individual scents – Acta Zool. Sin. 48(1): 27–34.

Received after revising March 2008