Acta Theriologica 50 (1): 51–58, 2005.
PL ISSN 0001–7051

Food hoarding behaviour of large field mouse *Apodemus peninsulae*

Jiqi LU and Zhibin ZHANG*

Lu J. and Zhang Z. 2005. Food hoarding behaviour of large field mouse *Apodemus peninsulae*. Acta Theriologica 50: 51–58.

An important behavioural adaptation for animal species with variable or unpredictable food availability is storing food. Food availability for large field mouse *Apodemus peninsulae* (Thomas, 1907) is not reliable. We conducted a series of tests with the large field mouse to determine food hoarding behaviour, response when their hoarded food was removed, and whether perishable foods were treated different than non perishable foods. The study was conducted in four semi-natural enclosures (4 × 3 × 1 m), established on the Donglingshan Mountain near Beijing, China. Thirteen large field mice were placed in enclosures and offered wild apricot *Prunus armeniaca* seeds and Liaodong oak *Quercus liaotungensis* acorns. Our results indicated that although large field mice hoarded seeds in larder and scatter patterns, they more frequently exhibited larder hoarding. Liadong oak acorns were generally consumed near the feeder, whereas apricot seeds were more frequently transported to the nest box. Only apricot seeds were scattered among hoard sites. When seeds were removed from hoarding sites the mice responded by taking increased amounts of seeds to their nest for larder and scatter hoarding. Hoarding sites were not randomly distributed throughout the enclosure.

State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, No. 25 Beisihuanxi Road, Haidian District, Beijing 100080, China, e-mail: zhangzb@ioz.ac.cn (JL, ZZ); College of Life Science, Henan Normal University, Xinxiang 453002, China, e-mail: roadjq@163.com (JL)

Key words: *Apodemus peninsulae*, food hoarding, food selection, hoarding strategy, China

Introduction

The large field mouse *Apodemus peninsulae* (Thomas, 1907) is a small Palaearctic rodent common across China, Korea, and Japan (Shou 1962, Chen *et al.* 2002). The mouse is commonly found in several habitats including coniferous and deciduous forests, shrubby areas, grasslands and abandoned cultivated fields. Their diet consists primarily of seeds from a variety of plants. Although, hoarding by the large field mouse has been reported (Shou and Li 1959, Shou, 1962), specifics pertaining to this behaviour are largely unknown.

Food storage is an important behavioural adaptation for any animal with variable or unpredictable food availability (Smith and Reichman 1984, Vander Wall 1990). Animals generally follow one of two strategies when hoarding food. Storing large quantities of food in a central location, such as a burrow or near

*Corresponding author

their nest, is referred to larder hoarding. While creating many small caches across a relatively large, perhaps throughout their home range, is called scattered hoarding. Vander Wall (1990) conducted a thorough review of the literature describing food hoarding by a variety of species.

MacDonald (1976) posed a pilfering avoidance hypothesis stating that cache strategies displayed by animals reflects the likelihood that their caches would be pilfered. Practiced strategy reflects the potential for pilfering combined with an individual's ability to protect their caches. Wood mice and field mice (*Apodemus* spp.) are reported to hoard food in larder and scatter patterns (Jennings 1975, Imaizumi 1979, Jensen and Nielsen 1986). Potential for pilfering by conspecifics is largely affected by the size, age, gender, reproductive status (Clarke and Kramer 1994a, b) and dominance status (Jenkins and Breck 1998) of the individual hoarding food. For example, eastern chipmunks *Tamias stiatus* typically larder hoard food in home burrows, but females with young and juveniles exhibited scatter hoarding (Clarke and Kramer 1994a). A species or an individual's preferred strategy may change depending on recent experience (Vander Wall 1995). Merriam's kangaroo rat shifted from predominately scatter hoarding to a larder hoarding strategy after their caches were pilfered (Preston and Jacobs 2001). Rodents also appear to differentiate among foods that can be stored and those likely to perish. Grey squirrels *Sciurus carolinensis* consume weevil-infested acorns first and store uncontaminated acorns (Steele *et al*. 1996). When offered several foods the eastern woodrat *Neotoma floridana* immediately consumed highly perishable items, but cached less perishable items (Reichman 1988).

We conducted a series of tests to develop an understanding of caching behaviour of the large field mouse. First, we identified their preferred hoarding strategy (larder versus scatter). Next, we determined whether they altered this strategy when stored food was removed from their caches. We also determined whether large field mice exhibit different behaviour when offered perishable foods then they did with non-perishable foods.

Study area

The study was conducted near Liyuanling village (40°00'N, 115°30'E; 1100 m a.s.l.) approximately 120 km northwest Beijing. This area's natural ecosystem has been severely disturbed due to extensive harvests and grazing by livestock (Chen 1992, 1997). Since 1990's, all villagers vacated from the village for restoration and conservation of local ecosystem. This Donlingshan Mountain region has a warm temperate continental monsoon climate. Predominate vegetation includes Liaodong oak, wild apricot, shrubs (*Vitex negundo*, *Prunus davidiana*), common grasses (*Elymus excelsus*, *Poa* spp., *Elsholtzia stauntoni*) and small patches of larch *Larix principis-rupprechtii*, and China pine *Pinus tabulaeformis*. The area is considered within the natural distribution region of large field mice (Shou 1962, Chen *et al*. 2002).

Material and methods

Adult large field mice (9 males, 4 females; mean (± SD) body mass = 28.38 ± 6.51 g) were live captured in the study area. Their previous dietary experience was presumed to have consisted primarily of the predominate vegetation. When captured, animals were weighed, examined to ensure they were healthy and to determine gender and tagged for subsequent identification. All subjects were individually maintained in plastic cages (37 × 26 × 17 cm) covered with a stainless steel mesh. The cage bottoms were covered in a layer of fine sawdust for bedding. Animals were given free access to rabbit pellets and water throughout the holding period. Lighting reflected natural day lengths during the study period from September through October, 2002.

Four enclosures (4 × 3 m) were constructed on an abandoned cultivated field. Iron sheets (1 m) were buried 30 cm deep to prevent subjects from digging underneath and tops were covered with strips of wire mesh (2.5 × 2.5 cm) to prevent them from crawling over. All vegetation was removed leaving the enclosure floor barren. A wooden nest box (30 × 20 × 20 cm) was placed in a corner of each enclosure. All food items were provided in a wooden feeder located at the enclosure center. The central feeder location forced animals to cross open ground to acquire food items and then again to potential hoarding sites. The water bottle was placed next to the nest box. Enclosures were divided in four equal quadrants with the feeder as the origin to ease mapping cache locations.

Foods offered mice during the study were wild apricot seeds and Liaodong oak acorns. We selected these foods because they are similar in size and they are important staples in the diets of large field mice in our study area. They also are large making them readily visible and easy to experimentally manipulate. Mice caught in the area were presumed to have had prior experience with both these foods. Wild apricot shrubs and Liaodong oak were common in the locale where subjects were captured. Wild apricot typically produces fruit from June to August, the fleshy epicarp rots then the seed falls to the ground. The exposed seed has a thick woody seed coat. Liaodong oak acorns are available from September through October. Its seed coat is fragile and some birds can open and eat the acorn (Wang and Ma 1999). Acorns also are invaded and consumed by insects and microbe (Steele *et al*. 1996, Sun and Chen 2000). Once infested acorns begin to decay and can perish quickly (Sun and Chen 2000).

We collected intact ripe wild apricot seeds and Liaodong oak acorns during the fruiting season. Apricot seeds were sun dried and acorns were dried in the shade then kept hermetically until used. Fresh mass (mean ± SD) of collected apricot seeds and acorns was 1.01 ± 0.24 g (n = 50) and 1.12 ± 0.30 g (n = 50), respectively. Individual seeds and acorns were tagged to facilitate finding them after they were moved by large field mice. Numbered metal tags were affixed with fine wire threaded through tiny holes drilled along the wild apricot spine or through the wider side of acorns. Subsequently seeds and acorns were easy to locate after mice transported and buried them because the metal tags would protrude above ground. Weight of the metal tags (0.1 g) was negligible relative to the weight of the food items. Previous studies indicated that attaching these tags did not significantly impact the transport and burial of tagged seeds by large field mice (Zhang and Wang 2001, Li and Zhang 2003).

A animal was randomly assigned to each of the four enclosures. Animals were food deprived for 6 hours prior to being placed in their respective enclosure and allowed 2.5 hours to adapt to their new environment. Twenty wild apricot seeds and 20 Liadong oak acorns were then placed in each centrally located feeder (day 0). After 24-hours (day 1) all food items were examined and location of pieces moved were identified and mapped. Food was recorded as fitting one of five categories: (1) eaten *in situ* of the feeder, (2) eaten after removed from the feeder, (3) buried within the enclosure, (4) stored in the nest, and (5) abandoned on the surface. Once data collection was completed all food items were removed from the enclosure. The procedures were then repeated with new 20 seeds and 20 acorns (day 2). Subjects were removed at the end of each trial and the nest box, feeder, and enclosure were thoroughly cleaned. An additional 4 mice were then randomly assigned to the enclosure and the test repeated. Subjects were tested only once.

We recognized larder hoarding and scatter hoarding as defined by others in prior experiments. Food items moved to a mouse's nest were regarded as larder hoarded (Smith and Reichman 1984, Jenkins and Breck 1998), while any food item buried was regarded as scatter hoarded (Vander Wall 1990).

SPSS for Windows (version 10.0) was employed to conduct statistical analyses. A separate Wilcoxon test was used to assess the difference (1) of seeds of wild apricot between larder and scatter hording, (2) of larder hoarded food items between seeds of wild apricot and Liaodong oak, (3) of larder hoarded food items between day 1 and day 2, and (4) of scatter hoarded food items between day 1 and day 2. Paired-sample t-test was used to determine (1) the differences of number of two types of seeds that were removed from the feeder between day 1 and day 2, and (2) the difference in the distances of scatter hoarded food items transported between day 1 and day 2. A Chi-square test was used to determine whether the buried seeds were distributed uniformly among quadrants within an enclosure, and a Kolmogorov-Smirnov test was used to determine whether the transport distance of buried apricot seeds fits a normal distribution pattern.

Results

Hoarding strategy

Although not statistically significant, during the first day animals tended to move more apricot seeds to their nest box than they buried (Table 1; Wilcoxon test: $z = -1.126$, $p = 0.260$). Mice did not bury any of the acorns, but carried several (1.31 ± 2.02) back to their nest (Table 1). Therefore, we conclude that larder hoarding was the preferred storage strategy of large field mice when placed in an unfamiliar environment.

Nonetheless, some mice used a scatter strategy as some apricot seeds were buried. These seeds were always buried alone, no caches were uncovered with more than a single seed. Buried sees were not randomly distributed among quadrants (Fig. 1; Chi-square test: $\chi^2 = 21.9104$, df = 3, $p < 0.0001$). The mean distance between the feeder and buried seeds was 141.84 ± 58.24 cm, and the distance seeds were moved fit a normal distribution pattern (Fig. 2; Kolmogorov-Smirnov test: $D = 0.570$, $p = 0.902$).

Table 1. Number of different hoarding patterns observed in large field mice in relation to two food types on day 1 (before pilferage) and day 2 (after pilferage). Sample size was 13 in all cases.

Behavioural category	Day 1			Day 2		
	Mean ± SD	Range	Total number of seeds	Mean ± SD	Range	Total number of seeds
			Wild apricot			
Stored in the nest	3.9 ± 4.6	0–15	51	7.8 ± 6.4	0–20	102
Buried	2.4 ± 4.5	0–15	31	3.0 ± 3.4	0–9	39
Abandoned on surface	1.1 ± 1.3	0–4	14	1.3 ± 1.5	0–5	17
Eaten *in situ*	0 ± 0	0	0	0 ± 0	0	0
Eaten after removal	0.6 ± 1.4	0–5	8	0.2 ± 0.6	0–2	2
			Liaodong oak			
Stored in the nest	1.3 ± 2.0	0–10	17	2.7 ± 3.2	0–8	35
Buried	0 ± 0	0	0	0 ± 0	0	0
Abandoned on surface	0.4 ± 0.7	0–2	5	0.5 ± 1.1	0–3	7
Eaten *in situ*	0.6 ± 1.1	0–4	8	0.9 ± 1.5	0–5	11
Eaten after removal	1.2 ± 1.5	0–5	16	1.4 ± 1.8	0–5	18

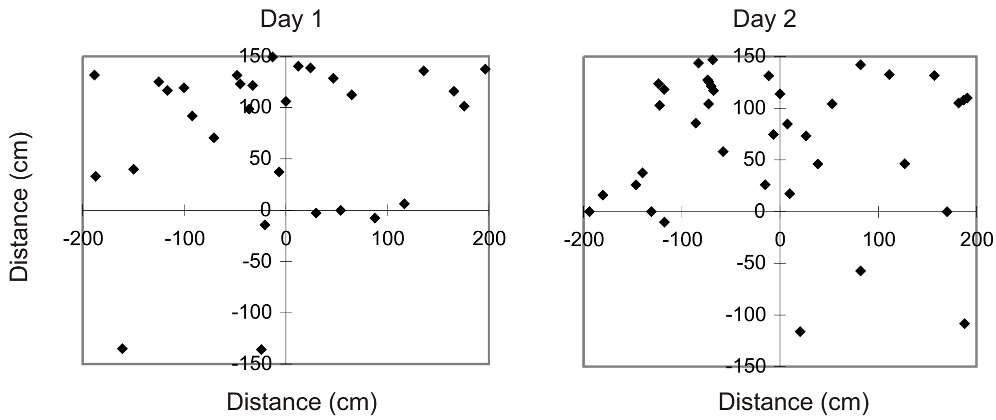

Fig. 1. Distribution pattern of seeds of wild apricot buried by large field mice within the enclosure. Feeder was placed at center with a coordinate of (0, 0), the nest box was placed at top left corner.

Pilferage response

All food items were removed from the enclosure after 24 hours which had simulated pilfering by other mice. Although not statistically significant, mice tended to hoard more apricot seeds on day 2, post perceived pilfering, than they had on day 1 (Table 1; $z = -1.738$, $p = 0.082$). However, on day 2 there were statistically more seeds stored in the nest than buried ($z = -2.091$, $p = 0.037$). Cache size of apricot seeds on day 2 again was limited to a single seed. Scatter hoarded seeds were not randomly distributed (Fig. 1; $\chi^2 = 24.1496$, df = 3, $p < 0.0001$). Mean distance mice buried seeds from the feeder station on day 2 was 139.72 ± 48.82 cm and this distance fit a normal distribution pattern ($D = 0.587$, $p = 0.881$). The mean distance seeds were buried from the feeder on day 1 was similar to the distance they were moved on day 2 (Fig. 2; t-test: $t = 0.574$, df = 38, $p = 0.570$). Again any acorns transported by mice on day 2 were eaten or moved to the nest, none of the acorns were buried.

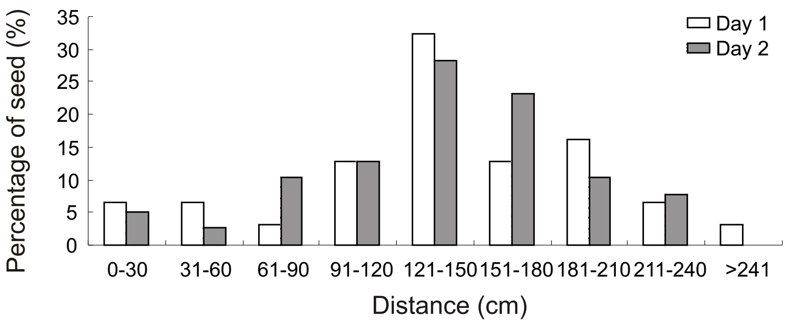

Fig. 2. Percentage distribution of wild apricot seeds transported and buried by large field mice in the enclosure at different distances from the feeder.

Food difference

In overall, there were significant more seeds of wild apricot than Liaodong oak were taken away from feeder on day 1 (Paired-sample *t*-test: $t = -2.465$, $p = 0.030$) and day 2 ($t = -3.558$, df = 12, $p = 0.004$). Large field mice stored Liaodong oak acorns and apricot seeds in their nest box, but only apricot seeds were buried (Table 1). Although not statistically significant, mice moved more apricot seeds to their nest than acorns on both day 1 ($z = -1.844$, $p = 0.065$) and day 2 ($z = -2.805$, $p = 0.005$). However, mice tended to eat more acorns than apricot seeds. Mice only ate Liaodong oak acorns in the feeders, and there also were more acorns eaten away from the feeder than apricot seeds on day 1 (statistically insignificant) and on day 2 ($z = -2.449$, $p = 0.014$). Simulated pilfering did not appear to impact the number of acorns eaten at the feeder.

Discussion

Large field mice exhibited both scatter and larder hoarding strategies. These results are similar to those demonstrated for other *Apodemus* species (Imaizumi 1979), and confirm prior field observations of large field mice behaviours (Shou and Li 1959, Shou 1962). Large field mice generally do not hibernate and are active throughout the winter (Shou 1962). A dual storage strategy may enhance their ability to survive a long winter when available food is scarce. Larder hoarder permits them to guard some food from pilfering, while scatter hoarding provides potential resources if their nest is overtaken or destroyed.

Large field mice took more food items on day 2 than they had on day 1. This was perhaps a response to perceived pilfering of their food caches. Additional apricot seeds and acorns were moved to the nest on day 2 than mice moved on day 1. When confronted with pilfering, other species have been observed storing additional food where it can be easily defended (Vander Wall 1990). Mice also buried more apricot seeds on the second day than they had buried on the first day. Animals incapable of defending a large cache are better served by making many small caches in a relatively wide area (Morris 1962, MacDonald 1976, Smith and Reichman 1984). Rather than changing hoarding strategy, animals increased the amount of food stored. This response may have been an effort to replace lost cached food and protect against a diminishing food supply. Alternatively, familiarity with the enclosure, including a food source, increased from day 1 to day 2. The increase in food hoarding may merely reflect less time spent exploring their surroundings and more time devoted to gathering food.

Several factors may affect the hoarding strategy of an animal. How an animal responds to a food item can be affected by the ease in which it can be immediately consumed (Jacobs 1992) and its storage potential (Reichman 1988, Vander Wall 1990, 1995, Post and Reichman 1991, Jacobs 1992). During our study mice consumed acorns at the feeder, but they did not eat apricot seeds there. Mice may have been limiting exposure at the more open feeder site. Other animals are reported to restrict feeding where such activities increase predation risk (Jacobs 1992, Clarke and Kramer 1994a, Lima 1998).

Mice also ate more acorns that had been moved to their nest than they did apricot seeds. Perhaps this depicts an expression of relative preference between the two food items. However, it also may reflect the poorer storage potential of acorns than apricot seeds. Liadong oak acorns rapidly deteriorate once infected by insects (Sun and Chen 2000) which are attracted to acorns (Steele *et al*. 1996). Mice in our study probably had prior experience with insect infested and decaying acorns. Prior studies reported the percentage of Liaodong oak acorns on the study site infested with weevils as high as 45.4% (Yu *et al*. 2001). Therefore, it is possible that mice consumed more oak acorns because they had learned the futility of trying to retrieve cached acorns. Conversely, the hard woody coat encompassing wild apricot seeds inhibited penetration by insects and microbes protecting cached seeds from damage.

Large field mice buried most apricot seeds along the base of enclosure walls or near their nest (Fig. 1). Mice may have been moving seeds as far from the feeder as possible within our enclosures. However, it also is possible mice may have been selecting sites which provided the most cover. Cover was limited in experimental enclosures because all vegetation had been removed. Therefore, the best available cover was along a wall or next to nest box, for sites where seeds were buried.

Our study provided further evidence that large field mice cache food and their caching strategy incorporates both scatter and larder hoarding. The selected strategy probably reflects experience and the available foods. We detected differential responses to the two types of seeds offered in our study. The more easily eaten acorn was more frequently consumed at the food dispersal point than were apricot seeds. Apricot seeds were more likely to be cached. Our enclosure experiment enabled us to isolate animals and control food resources permitting a detailed and specific look at individual behaviour. However, additional field tests will be necessary to fully understand the hoarding behaviour of the large field mouse.

Acknowledgements: We thank Mr C.-G. Yi, Mr F.-S. Wang, and Dr H.-J. Li for their assistance in our study. This study was supported by the key projects (FS 2000-009, G2000046802) of the Ministry of Science and Technology of China, and the key project (KSCX2-SW-103) of the Chinese Academy of Sciences, and the 'Bai Ren Ji Hua' Program of Chinese Academy of Sciences.

References

Chen L. Z. 1992. The oak forest in north China. Braun-Blanquetia 8: 33–37.

Chen L. Z. 1997. The importance of Dongling Mountain region of warm temperate deciduous broad-leaved forest. [In: Structure and function of warm temperate forest ecosystem. L. Z. Chen and J. H. Huang, eds]. Science Press, Beijing: 1–9. [In Chinese with English abstract]

Chen W., Gao W. and Fu B. Q. (eds) 2002. [Mammalian fauna of Beijing]. Beijing Press, Beijing: 249–254. [In Chinese]

Clarke M. F. and Kramer D. L. 1994a. The placement, recovery, and loss of scatter hoards by eastern chipmunk, *Tamias striatus*. Behavioural Ecology 5: 353–361.

Clarke M. F. and Kramer D. L. 1994b. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. Animal Behaviour 48: 299–308.
Imaizumi Y. 1979. Seed storing behavior of *Apodemus speciosus* and *Apodemus argentatus*. Zoological Magazine, Tokyo 88: 43–49.
Jacobs L. F. 1992. The effect of handling time on the decision to cache by gray squirrels. Animal Behaviour 43: 522–524.
Jenkins S. H. and Breck S. W. 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79: 1221–1233.
Jennings T. J. 1975. Notes on the burrow systems of woodmice (*Apodemus sylvaticus*). Journal of Zoology, London 177: 500–504.
Jensen T. S. and Nielson O. F. 1986. Rodents as seed dispersers in a heath-oak wood succession. Oecologia 70: 214–221.
Li H. J. and Zhang Z. B. 2003. Effects of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz). Forest Ecology and Management 176: 387–396.
Lima S. L. 1998. Stress and decision making under the risk of predation: Recent development from behavioral, reproductive, and ecological perspectives. Advance in the Study of Behavior 27: 215–290.
MacDonald D. W. 1976. Food caching by red foxes and other carnivores. Zeitschrift für Tierpsychology 42: 170–185.
Morris D. 1962. The behaviour of the green acouch (*Myoprocta pratti*) with special reference to scatter-hoarding. Proceedings of Zoological Society of London 139: 701–732.
Post D. M. and Reichman O. J. 1991. Effects of food perishability, distance and competitors on caching behavior by eastern woodrats. Journal of Mammalogy 72: 513–517.
Preston S. D. and Jacobs L. F. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. Behavioural Ecology 12: 517–523.
Reichman O. J. 1988. Caching behavior by eastern woodrats, *Neotoma floridana*, in relation to food perishability. Animal Behaviour 36: 1525–1532.
Shou Z. H. and Li Q. T. 1959. [Preliminary investigation on the rodent fauna in cut-over land of different years in Dailing Frest Region of Xiaoxing'an Mountains]. Chinese Journal of Zoology 3: 6–11. [In Chinese]
Shou Z. H. 1962. [The mammal of economics significance in China]. Science Press, Beijing: 230–234. [In Chinese]
Smith C. C. and Reichman O. J. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15: 329–351.
Steele M. A., Hadj-Chikh L. Z. and Hazsltine J. 1996. Caching and feeding decisions by *Sciurus carolinensis*: responses to weevil-infested acorns. Journal of Mammalogy 77: 305–314.
Sun S. C. and Chen L. Z. 2000. Seed demography of *Quercus liaotungensis* in Dongling mountain region. Acta Phytoecologica Sinica 24: 215–221.
Vander Wall S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago: 1–445.
Vander Wall S. B. 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. Oikos 74: 533–537.
Wang W. and Ma K. P. 1999. Predation and dispersal of *Quercus liaotungensis* acorns by Chinese rock squirrel and Eurasian jay. Acta Botonica Sinica 41: 1142–1144. [In Chinese with English abstract]
Yu X. D., Zhou H. Z., Luo T. H., He J. J. and Zhang Z. B. 2001. Insect infestation and acorn fate in *Quercus liaotungensis*. Acta Entomologica Sinica 44: 518–524. [In Chinese with English abstract]
Zhang Z. B. and Wang F. S. 2001. Effects of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). Acta Ecologica Sinica 21: 839–845.

Received 11 June 2003, accepted 12 October 2004.

Associate Editor was Leszek Rychlik.