Original article

Endocarp thickness affects seed removal speed by small rodents in a warm-temperate broad-leafed deciduous forest, China

Hongmao Zhang[a,b,c], Zhibin Zhang[a,*]

[a]State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology,
The Chinese Academy of Sciences, Datun Road, Chaoyang District, Beijing 100101, China
[b]College of Fisheries, Huazhong Agricultural University, Wuhan 430070, China
[c]Graduate School of the Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

ABSTRACT

Seed traits are important factors affecting seed predation by rodents and thereby the success of recruitment. Seeds of many tree species have hard hulls. These are thought to confer mechanical protection, but the effect of endocarp thickness on seed predation by rodents has not been well investigated. Wild apricot (*Prunus armeniaca*), wild peach (*Amygdalus davidiana*), cultivated walnut (*Juglans regia*), wild walnut (*Juglans mandshurica* Maxim) and Liaodong oak (*Quercus liaotungensis*) are very common tree species in northwestern Beijing city, China. Their seeds vary greatly in size, endocarp thickness, caloric value and tannin content. This paper aims to study the effects of seed traits on seed removal speed of these five tree species by small rodents in a temperate deciduous forest, with emphasis on the effect of endocarp thickness. The results indicated that speed of removal of seeds released at stations in the field decreased significantly with increasing endocarp thickness. We found no significant correlations between seed removal speed and other seed traits such as seed size, caloric value and tannin content. In seed selection experiments in small cages, Père David's rock squirrel (*Sciurotamias davidianus*), a large-bodied, strong-jawed rodent, selected all of the five seed species, and the selection order among the five seed species was determined by endocarp thickness and the ratio of endocarp mass/seed mass. In contrast, the Korean field mouse (*Apodemus peninsulae*) and Chinese white-bellied rat (*Niviventer confucianus*), with relatively small bodies and weak jaws, preferred to select small seeds like acorns of *Q. liaotungensis* and seeds of *P. armeniaca*, indicating that rodent body size is also an important factor affecting food selection based on seed size. These results suggest endocarp thickness significantly reduces seed removal speed by rodents and then negatively affects dispersal fitness of seeds before seed removal of tree species in the study region. However, effect of endocarp thickness on final dispersal fitness needs further investigation because it may increase seed caching and survival after seed removal.

© 2008 Elsevier Masson SAS. All rights reserved.

---

* Corresponding author. Tel.: +86 10 6480 7213; fax: +86 10 6480 7099.
  E-mail address: zhangzb@ioz.ac.cn (Z. Zhang).

1.   Introduction

Granivory by rodents has been identified as a key process affecting the survival and recruitment of plants in temperate ecosystems (Kerley and Erasmus, 1991; Li and Zhang, 2003; Lu and Zhang, 2004; Xiao et al., 2005a). Although rodents consume large proportions of seed crops of many plants (e.g. Iida, 1996; Li and Zhang, 2003; Lu and Zhang, 2005a), they also have important positive impacts on seedling establishment and plant regeneration by scattering buried seeds in soil away from the parent plants (Vander Wall, 1990, 2003). Those seeds are not removed from parent plants often suffer higher predation and the subsequent seedlings often suffer higher density-limited mortality. Thus, seed removal by rodents has direct influences on dispersal fitness before seed caching, and thus has important impacts on regeneration and colonization in plant populations, and hence on plant community structure (Zhang et al., 2008).

Many factors, such as seed traits, spatio-temporal variation and the composition of vegetation, can affect seed removal by rodents (e.g. Vander Wall, 1990; Li and Zhang, 2003, 2004). The qualities of seeds and fruits are important factors affecting which seeds rodents choose to remove and eat (Vander Wall, 1990), and knowledge of the physical and chemical attributes of the seeds which are selected by rodents provides a basis for the prediction of whether seeds of a species are likely to be preyed on by rodents (Kelrick and MacMzhon, 1985). Several seed traits affecting seed removal by rodents have been identified, e.g. seed size and mass (Price, 1983; Eriksson, 1999; Jakobsson and Eriksson, 2000; Moles and Westoby, 2003; Xiao et al., 2005a), handling time (Kaufman and Collier, 1981), and content of moisture content (Frank, 1988; Hulbert and Macmillen, 1988), energy and soluble carbohydrates (Kelrick et al., 1986; Jenkins, 1988; Kerley and Erasmus, 1991; Xiao et al., 2005b), other nutrients (e.g. protein and fat) (Izhaki, 2002), and secondary chemical compounds (e.g. tannins and other polyphenols) (Steele et al., 1993). Seeds of many tree species have a hard coat (e.g., a woody endocarp). This trait would not be expected to favor their removal or consumption by rodents, because gnawing a hard coat not only increases the energy expenditure required to carry or eat the seeds but also, by increasing the time required to handle seeds, increases their predation risk. Ganesh and Davidar (2005) reported that seed predation levels varied from 1% to almost 96% among 35 tree species, and that seed coat thickness was important in influencing patterns of seed selection. In an enclosure, both Chinese white-bellied rat (Niviventer confucianus Muridae) and The Korean field mouse (Apodemus peninsulae Muridae) preferred to eat seeds of Liaodong oak (Quercus liaotungensis) (with very thin and fragile endocarps) in situ and to cache seeds of Wild apricot (Prunus armeniaca) (with woody endocarps) (Lu and Zhang, 2005c,d). These results indicated that seed protection, as estimated by endocarp thickness, showed a significant effect in lowering seed predation.

Wild apricot (P. armeniaca), wild peach (Amygdalus davidiana), cultivated walnut (Juglans regia), wild walnut (Juglans mandshurica) and Liaodong oak (Q. liaotungensis) are very common tree species in the Dongling Mountains, about 120 km northwest of Beijing city, China. Their seeds have woody endocarps and vary greatly in size, endocarp thickness, tannin content and caloric value. Seeds of both J. mandshurica (fresh weight: 5.0–9.0 g) and J. regia (6.0–11.0 g) are large and their endocarps are very hard. Seeds of both A. davidiana (2.0–5.0 g) and P. armeniaca (1.0–3.0 g) are small but their endocarps are also very hard. Acorns of Q. liaotungensis (1.5–4.5 g) are small and their endocarp is very thin and fragile. Apodemus peninsulae, N. confucianus and Père David's rock squirrel (Sciurotamias davidianus Sciuridae) are common seed predators in the study region. Sciurotamias davidianus is very large (adult body mass: 200–260 g), N. confucianus is medium-sized (adult body mass: 63–77 g), and A. peninsulae is very small (adult body mass: 20–28 g).

The purpose of this study was to assess the role of seed endocarp thickness and rodent body size on seed removal. We were especially interested to determine whether the effect of seed endocarp thickness interacted with that of seed size. We artificially released intact cleaned seeds (without pulps) of the above five tree species in the field during three seasons. Selection of seeds of the five tree species by the above three rodent species was also observed in cage experiments. Because rodents should be at greater predation risk and suffer greater energy loss when they carry or eat seeds with a hard coat, we predicted that seeds with a thick endocarp would have low levels of removal. Because seed removal and consumption may be limited by rodent body size, we predicted that large rodent species would eat or remove seeds of a broader range of size or mass than would small rodent species.

2.   Methods

2.1.   Study site

This study was carried out near Liyuanling village in the Mentougou District, a mountainous area in the Dongling Mountains northwest of Beijing city, China (40°00′ N, 115°30′ E). Altitude of the study site is about 1 140 m; the study site is characterized by a temperate continental monsoon climate. The main types of landscape in this area are composed of shrublands, abandoned farmlands and secondary forests, all of which have been heavily disturbed by local residents and domestic animals during the last several decades. Quercus liaotungensis, J. mandshurica, P. armeniaca, and A. davidiana are dominant tree species (Li and Zhang, 2003, 2007; Lu and Zhang, 2004, 2005a), and some Chinese pine (Pinus tabulaeformis) has been sparsely planted in cropland. Our focal tree species are very common in our study area; P. armeniaca and Q. liaotungensis are more widespread than J. mandshurica, A. davidiana and J. regia. Seeds of P. armeniaca and A. davidiana mature and fall from mid-July to mid-August, while seeds of Q. liaotungensis, J. regia and J. mandshurica mature in late August and fall within the next 30 days. Pulps surrounding seeds of these species are not used by rodents and no animals prey upon these seeds before they mature.

2.2.   Selection of experimental plot

An area of about 7.5 ha was chosen as our experimental plot on a southwest-facing slope (of 30°–45°). The main habitats

are secondary broad-leafed deciduous forests, which connect with a few shrubland and abandoned farmland habitats at the foot of the slope. *Quercus liaotungensis* and *P. armeniaca* are the dominant plant species and their average height is 5.0 ± 2.2 m ($n = 100$). Additionally, some patches of young *Q. liaotungensis* shrubs and some *J. mandshurica*, *J. regia* and *A. davidiana* trees are sparsely distributed in the plot. The total coverage of trees and shrubs is over 80%. Within the plot three parallel transects were established about 20 m apart along the slope from the foot to the top; 20 experimental stations (0.5 m² for each) 10–15 m apart along each transect were sampled as our seed release stations.

2.3. Seed collection and releasing in fields

During the seedfall period of the five experimental tree species in 2004, fresh and intact cleaned seeds were collected from the ground outside our experimental plot and kept in a dry and ventilated place to prevent rotting, mildew and germination. Seeds of all five species depended almost entirely on rodents for dispersal because of their hard woody endocarps (Lu and Zhang, 2004, 2005a,b,c). Some birds, e.g., the Eurasian jay (*Garrulus glandarius*) (Li and Zhang, 2003, 2004), eat a few seeds of *Q. liaotungensis*, but their effects are negligible because they are very rare in our study area and hardly prey on acorns under the canopy.

Intact cleaned seeds of the five species were chosen randomly for field experiments. On May 5, Jul. 5 and Sep. 5, 2005, 20 seeds of each species were placed on the ground surface together at each seed station. The total number of seeds released in three seasons was 3 (transects) × 20 (stations) × 100 (seeds) × 3 (seasons) = 18,000 seeds. The number of seeds that intact or eaten by rodents (fragments of endocarps or seed kernel were found scattered at the seed stations) at each station was recorded from 9:00 am to 11:00 am everyday for 16 days. "Seed removal" was scored as the fate of seeds that were removed by small rodents from the seed stations, and "seed survival" was scored as the fate of seeds that were left intact at the seed stations. Seed survival time at seed stations is a measure of speed of seed removal by rodents in field. Those seeds that were eaten by small rodents at seed stations were regarded as eaten *in situ*.

2.4. Seed traits

Fifty intact seeds (each seed includes endocarp and kernel) of each species were selected randomly for measurement of morphological traits in the laboratory. Seed mass, kernel mass and endocarp mass of individual seed were weighed with an electronic scale (precision ± 0.01 g) after drying at 80 °C for 24 h in a constant temperature stove. The percentage of seed coat mass/seed mass was calculated. Seed length, width, and endocarp thickness were measured with a vernier caliper (precision ± 0.02 mm). Because the hard woody endocarps of our focal seed species are similar in texture, the endocarp thickness and endocarp mass/seed mass were used to reflect the mechanical defense ability of a given seed. Mechanical protection should be expected to increase with endocarp thickness and the ratio endocarp mass/seed mass. Some (20–50) dry intact cleaned seeds of each species were

selected randomly as samples for measurement of nutritional traits. Percentages of crude protein, crude fat, crude starch, crude fiber and tannin of the seeds were measured by the Cereal Quality Supervision and Testing Centre, Ministry of Agriculture, China (No. 12, Southern Zhongguancun Road, Haidian District, Beijing). To estimate the maximum energetic benefit of each seed species for consumers, the caloric values of seeds were calculated by the average gross energy equivalents of protein (17.2 KJ/g), fat (38.9 KJ/g), and carbohydrates (17.2 KJ/g) (Yang, 2002), and caloric value per seed using mean kernel mass × caloric value. The caloric value and caloric value per seed were used to reflect the nutritional value, and the tannin content was used to reflect the chemical defense of each seed species.

2.5. Key rodents and their morphological traits

At the end of the day-by-day checking for each experiment (May 21, July 22 and September 19, 2005), 40 live traps (12 × 12 × 25 cm, made of steel wire, placed 5 m apart and open to one direction) baited with peanuts were placed along each of three experimental transects to determine the rodents that could potentially remove the released seeds. The traps were checked every dawn and dusk and those with captured rodents were replaced with new ones. After recording species and sex, the captured rodents were released immediately *in situ*. This experiment continued over 4 days. The total number of trap-days was 40 (traps) × 4 (days) × 3 (transects) × 3 (seasons) = 1440.

The morphological traits of the key rodent species (19 *A. peninsulae*, 26 *N. confucianus* and 17 *S. davidianus*) were measured. These rodents were captured with live traps at least 1500 m away from our experimental plot, to avoid effects of trapping on rodent population density in the experimental plot, and killed in the laboratory. The body mass, mass of the masseter muscle (a measure of jaw strength), and body length of rodents of the three species were recorded to assess their seed handling abilities. A rodent with a larger body and a stronger masseter should have a greater ability to handle large and/or hard seeds.

2.6. Seed selection experiments in cages

Captured *A. peninsulae* and *N. confucianus* were fed in special plastic boxes (37 × 26 × 17 cm), while *S. davidianus* were caged in special wire cages (80 × 80 × 100 cm) individually at ambient temperature and photoperiod with abundant commercial mouse feed and water. All of the fed rodents were captured with live traps at least 1500 m apart from the experimental plot, to avoid affecting rodent population density in the plot. Sixteen (adults, eight male and eight female) individuals of each rodent species were chosen for the seed feeding experiment in cages after being housed for 2 weeks. Their initial body weights were 63–77 g for *N. confucianus*, 20–28 g for *A. peninsulae*, and 200–260 g for *S. davidianus*. All experimental animals were deprived of food for 12 h and all experimental cages were cleaned before the experiment to avoid the effects of previous food on their seed selection. Ten intact seeds of each species were supplied together for each mouse to select randomly. In the following 4 days, the seeds provided were

Table 1 – Population abundance and compositions of rodent species in the study area

Season	Traps	Niviventer confucianus	Apodemus peninsulae	Sciurotamias davidianus	Apodemus agrarius	Tscherskia triton	Tamias sibiricus	Total	Trap success %
Spring	480	7	6	2	1			16	3.3
Summer	480	16	24	7		10	1	58	12.1
Autumn	480	17	16	5		5		43	9.0
Total	1440	40	46	14	1	15	1	117	8.1
Proportion %		34.2	39.3	12.0	0.9	12.8	0.9	100	

checked every noon and the seed selection by each mouse was recorded. Any seed eaten or hoarded in the nest or in the corner of the feeding box was regarded as having been "selected" by rodents.

2.7. Statistics and analysis

SPSS for Windows (Version 13.0) was used for statistical analysis. Survival dynamics of released seeds at seed station in different seasons were analyzed individually with Cox regression. The median survival times of seeds of each species both at seed stations in three seasons and in cages were analyzed with Life Table. Both at seed stations and in cages, the correlations between the median survival times of seeds and seed traits were analyzed separately with Pearson correlation tests. Differences in survival time of different seeds at releasing stations in different seasons and differences in seed removal by the three rodent species in cages were tested individually with Friedman tests.

3. Results

3.1. Key rodents and their morphological traits

A total of 117 individuals of six rodent species were captured (Table 1). Among them, A. peninsulae accounted for 39.3%;

N. confucianus, 34.2%; Tscheskia triton, 12.8%; and S. davidianus, 12.0%. These four rodent species are common and the other two rodent species, Apodemus agrarius and Tamias sibiricus, were relatively rare in the study area. Tscheskia triton mostly occurs in croplands near the forests, and the other rodent species mostly inhabit forests or shrublands.

The body length, body mass and masseter mass of A. peninsulae were 98.8 ± 5.1 mm, 23.6 ± 4.1 g and 0.13 ± 0.02 g (mean $\pm$ S.D, $n = 19$), respectively; those of N. confucianus were 135.2 ± 11.6 mm, 62.8 ± 10.0 g and 0.31 ± 0.03 g ($n = 26$), respectively; and those of S. davidianus were 210.2 ± 7.3 ($n = 26$), 222.1 ± 23.2 g and 0.51 ± 0.05 g ($n = 17$), respectively.

3.2. Seed traits

Seeds of the experimental species differed greatly in their morphological traits. Seeds of J. regia and J. mandshurica are larger and heavier than those of the three other species, A. davidiana and J. mandshurica have a thicker endocarp and a higher ratio of endocarp mass/seed mass than J. regia and P. armeniaca, and Q. liaotungensis has the thinnest and fragile endocarp and lowest endocarp mass/seed mass (Table 2). Seed caloric values decreased in the order J. regia, J. mandshurica, A. davidiana, P. armeniaca and Q. liaotungensis (Table 2), whereas their tannin contents decreased in the order Q. liaotungensis, J. regia, J. mandshurica, A. davidiana and P. armeniaca (Table 2).

Table 2 – Morphological and nutritional traits of the five seed species (mean ± S.D.) (– denotes no data). Twenty to 50 dry intact cleaned seeds of each species were used to measure crude protein, crude fat, crude starch, crude fiber and tannin. The caloric values of seeds were calculated by the average gross energy equivalents of protein (17.2 KJ/g), fat (38.9 KJ/g), carbohydrates (17.2 KJ/g), and caloric value per seed was calculated using mean kernel mass × caloric value

Seed traits	Quercus liaotungensis	Prunus armeniaca	Amygdalus davidiana	Juglans regia	Juglans mandshurica
Seed length (mm)	17.8 ± 2.8	22.1 ± 1.6	21.2 ± 2.0	30.5 ± 2.8	34.1 ± 2.4
Seed width (mm)	13.3 ± 2.1	9.8 ± 0.8	17.2 ± 2.0	29.6 ± 2.0	23.8 ± 2.0
Endocarp thickness (mm)	0.3 ± 0.1	1.1 ± 0.2	3.9 ± 0.6	1.2 ± 0.3	2.7 ± 0.5
Seed mass (g)	2.0 ± 0.9	1.2 ± 0.2	3.2 ± 0.6	9.1 ± 1.7	6.1 ± 1.0
Endocarp mass (g)	0.3 ± 0.1	0.8 ± 0.1	3.2 ± 0.6	4.8 ± 1.0	5.1 ± 0.9
Kernel mass (g)	1.7 ± 0.9	0.4 ± 0.1	0.4 ± 0.1	4.3 ± 0.9	1.0 ± 0.2
Endocarp mass/Seed mass (%)	14.8 ± 3.7	67.3 ± 5.9	87.9 ± 2.8	52.3 ± 5.3	83.6 ± 2.1
Crude protein (g/100 g)	11.5	25.1	29.0	15.4	28.1
Crude fat (g/100 g)	1.5	53.1	52.7	70.7	62.3
Crude starch (g/100 g)	34.1	–	–	–	–
Crude fiber (g/100 g)	4.1	2.9	3.0	1.4	1.0
Tannin (g/100 g)	8.6	0.1	0.1	0.6	0.5
Caloric value (KJ/g)	8.4	25.5	26.0	30.4	29.2
Caloric value per seed (KJ)	14.2	10.4	9.9	131.8	29.2

3.3. Seed removal by rodents in field

Nearly half of the *A. davidiana* seeds and a few *J. mandshurica* seeds still remained at the seed stations at the end of the experiment, while all released seeds of other species were removed by rodents within 16 days. Very few seeds were eaten *in situ* during the time of the experiment. In general, speed of seed removal by rodents decreased in the order *Q. liaotungensis* > *P. armeniaca* > *J. regia* > *J. mandshurica* > *A. davidiana* in all seasons (Fig. 1). The survival time of released seeds was significantly different among tree species (Wald = 1122.568, df = 4, $P < 0.001$) and seasons (Wald = 1712.081, df = 2, $P < 0.001$).

A Spring

B Summer

C Autumn

Prunus armeniaca   *Amygdalus davidiana*
Juglans mandshurica   *Juglans regia*
Quercus liaotungensis

Fig. 1 – Dynamics of removal of seeds released at seed stations in three seasons. Error bars are standard errors.

Seed removal speeds were highest in autumn, medium in summer and lowest in spring (Fig. 1). When seasons were analyzed separately, the differences of seed survival time among seed species were significant in all seasons ($\chi^2 = 54.350$, df = 4, $P < 0.001$ in spring, $\chi^2 = 57.653$, df = 4, $P < 0.001$ in summer and $\chi^2 = 54.203$, df = 4, $P < 0.001$ in autumn). The order of median survival time was *Q. liaotungensis* < *P. armeniaca* < *J. regia* < *J. mandshurica* < *A. davidiana* (Table 3). The median survival times of released seeds at seed stations were significantly and positively correlated with endocarp thickness in all three seasons, and significantly correlated with the ratio of endocarp mass/seed mass in spring (Table 4). Thus we concluded that endocarp thickness is the dominant factor determining seed removal in the field.
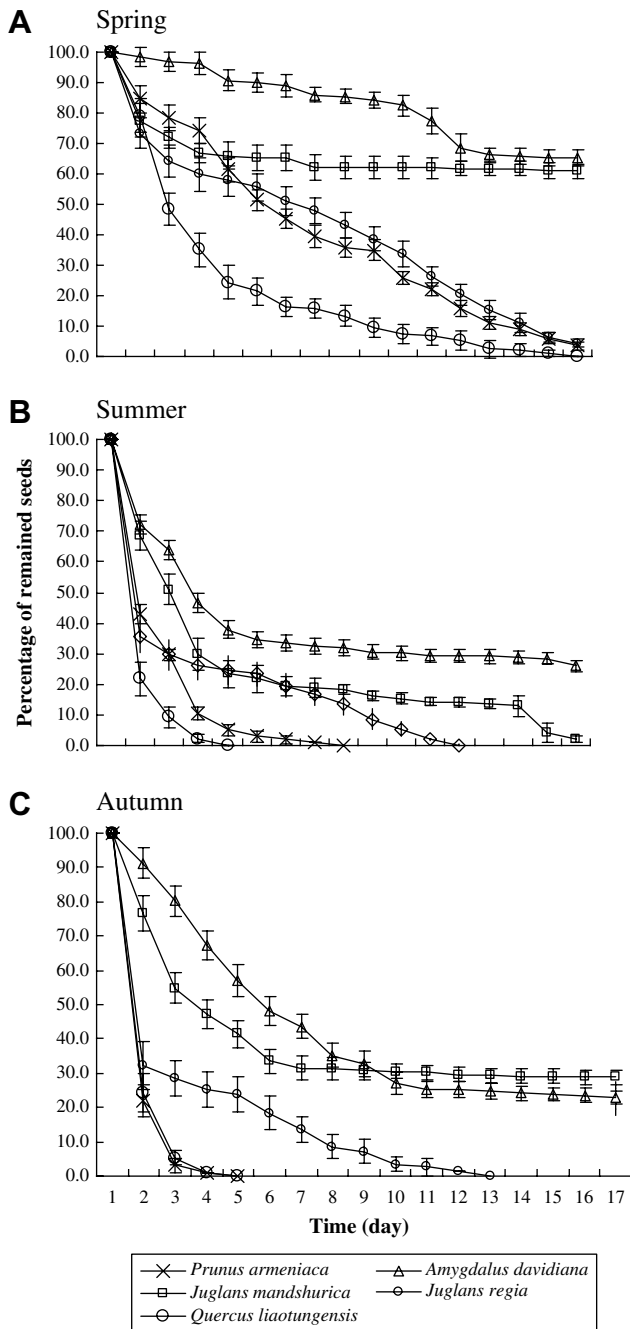
3.4. Seed selection in cages

Sciurotamias davidianus chose a broader range of seed species than *N. confucianus* and *A. peninsulae*. *Apodemus peninsulae* showed a preference for seeds of *Q. liaotungensis* and *P. armeniaca*, but showed no selection on *J. regia*, *J. mandshurica* and *A. davidiana* seeds ($\chi^2 = 15.351$, df = 4, $P = 0.004$) (Fig. 2A). *Niviventer confucianus* selected more seeds of *Q. liaotungensis* and *P. armeniaca*, few seeds of *J. regia* and *A. davidiana* and no seeds of *J. mandshurica* ($\chi^2 = 14.773$, df = 4, $P = 0.005$) (Fig. 2B). *Sciurotamias davidianus* consumed seeds of all five species, with a preference for seeds of *Q. liaotungensis* and *J. regia* ($\chi^2 = 16.000$, df = 4, $P = 0.003$) (Fig. 2C). The order of seed selection for *S. davidianus*, preference decreased following the order *Q. liaotungensis*, *J. regia*, *P. armeniaca*, *J. mandshurica* and *A. davidiana* (Fig. 2C), and the median survival time of these five seed species were significantly and positively correlated with the ratio of endocarp mass/seed mass ($r = 0.972$, $P = 0.005$). In general, endocarp thickness was still dominant in determining the order of seed selection in cages, but larger rodents were able to consume a wider range of seed species of different sizes. The order of seed selection by each of the three rodent species in the cage experiments corresponded well to that observed in the field except for the selection by *S. davidianus* which showed preference of *J. regia* to *P. armeniaca*

4. Discussion

4.1. Population abundance and composition of rodent species

Apodemus peninsulae, *N. confucianus*, *T. triton* and *S. davidianus* are common rodent species and attributed to seed removal in the field in the study area. In cage experiments, *A. peninsulae* and *N. confucianus* mainly selected seeds of *Q. liaotungensis* and *P. armeniaca*, while *S. davidianus* mainly selected seeds of *Q. liaotungensis*, *J. regia* and *P. armeniaca*. Seeds of *J. mandshurica* and *A. davidiana* were less selected by rodents. Although *A. agrarius* and *T. sibiricus* have been shown to remove seeds of *Q. liaotungensis*, *J. regia* and *P. armeniaca* in this area (unpublished data), their effects on seed removal might be limited because of their very low population numbers during the study period.

Table 3 – Median survival times (days) of seeds of the five species at seed stations in three seasons				
Season	Quercus liaotungensis	Prunus armeniaca	Amygdalus davidiana	Juglans regia	Juglans mandshurica
Spring	2.3	4.2	7.8	5.0	7.5
Summer	0.7	1.0	5.6	2.6	3.1
Autumn	0.6	0.7	5.6	2.0	4.7

Because of the hard endocarps of these species, seeds of *P. armeniaca*, *A. davidiana*, *J. mandshurica* and *J. regia* can only be consumed by rodents. Previous studies showed that some other animals, such as deer, wild pigs, cattle, Eurasian jay (*Garrulus glandarius*) and pheasant (*Phasianus cochicus*) might also eat acorns of *Q. liaotungensis* (Li and Zhang, 2003; Lu and Zhang, 2005a), but these animals were very rare in our study area and their effects can be neglected.

4.2.   Seasonal differences of seed removal speed

Speed of removal of seeds of these five tree species was much higher in autumn and summer than in spring (Table 3, Fig. 1). This observation further supports our previous studies in this area (Lu and Zhang, 2004; Li and Zhang, 2007). Seasonal variation of rodent population densities might be the major reason for seasonal differences in speed of seed removal. Live-trapping results suggested that rodent population densities were higher in summer (trap success 12.08%) and autumn (8.96%) than in spring (3.33%) (Table 1). Kollmann et al. (1998) reported that seed predation intensity decreased in the order summer > autumn > spring > winter; and that temporal fluctuation in rodent population densities were mostly responsible for this variation. The increased effort of rodents in food storage for over-wintering is also a likely cause of the rapid removal of seeds in autumn (Vander Wall, 1990; Lu and Zhang, 2004).

Seasonal variation of fruiting phenology might affect seasonal differences in seed removal because availability of alternative food in food-abundant seasons may slow the removal of the released seeds. Janzen (1971) and Sork (1983) showed that large crops could slow seed removal by satiating seed predator-dispersers. However, our results showed that the speed of seed removal varied significantly among seasons and was fastest in the food-richest season – autumn. The reason might be that the crops of our focal tree species in 2005 were low and rodent abundances were relatively high (unpublished data).

The order of removal of seeds of five tree species in the field did not differ among seasons, a finding that conforms to previous observations (Jensen, 1993; Kollmann et al., 1998; Xiao et al., 2006). Kollmann et al. (1998) found that rodents demonstrated species-specific selectivity among 12 fleshy-fruited species and that seed preferences were notably consistent among seasons and years.

4.3.   Effects of body size of rodents on seed removal speed

Rodents with different body size have different seed handling abilities, and therefore have different seed preferences (Rosenzweig and Sterner, 1970; Vieira et al., 2003; Lu and Zhang, 2005b,c). Small and medium-sized frugivores should be most attracted by small fruits or seeds (Izhaki, 2002). In Atlantic forests of Brazil, smaller rodent species (e.g. *Akodon serrensis*, *Oligoryzomys nigripes* and *Wilfredomys pictipes*) fed mainly on small to medium-sized seeds (<10 mm diameter), medium-sized rodents (e.g. *Oecomys* aff. *Concolor* and *Oryzomys russatus*) fed on seeds with diameter ≤15 mm, and larger rodents (e.g. *Trinomys ihberingi* and *Nectomys squamipes*) consumed seeds of most species independent of seed size (Vieira et al., 2003). The results of our seed selection experiments in cages supported this observation. *Apodemus peninsulae*, with a small body and small, weak masseter muscles, could hardly open hard endocarps and only selected relatively small and soft seeds (e.g., those of *Q. liaotungensis* and *P. armeniaca*) and rejected large and hard seeds (e.g., those of *J. regia*, *A. davidiana* and *J. mandshurica*). *Niviventer confucianus*, with intermediate body size and heavier masseter muscles, selected seeds of *Q. liaotungensis* and *P. armeniaca* and a few seeds of *J. regia* and *A. davidiana*, while *S. davidianus*, with the largest body

| Table 4 – Correlation coefficients (Pearson's R) between median survival times of seeds of different species released at seed stations, and seed traits with in three seasons. *Correlation was significant at the 0.05 level (2-tailed). **Correlation was significant at the 0.01 level (2-tailed)						
Seed traits	Spring		Summer		Autumn	
	r	P	r	P	r	P
Seed length	0.522	0.367	0.208	0.738	0.374	0.535
Seed width	0.403	0.501	0.355	0.558	0.371	0.538
Seed mass	0.335	0.581	0.269	0.661	0.272	0.658
Endocarp thickness	0.522*	0.011	0.950*	0.013	0.964**	0.008
Endocarp mass	0.742	0.151	0.590	0.295	0.668	0.218
Endocarp mass/seed mass	0.919*	0.027	0.731	0.161	0.776	0.123
Kernel mass	−0.276	0.653	−0.174	0.779	−0.289	0.638
Tannin	−0.734	0.158	−0.545	0.342	−0.503	0.388
Caloric value	0.720	0.170	0.509	0.381	0.497	0.394
Caloric value per seed	−0.040	0.950	−0.002	0.997	−0.122	0.845
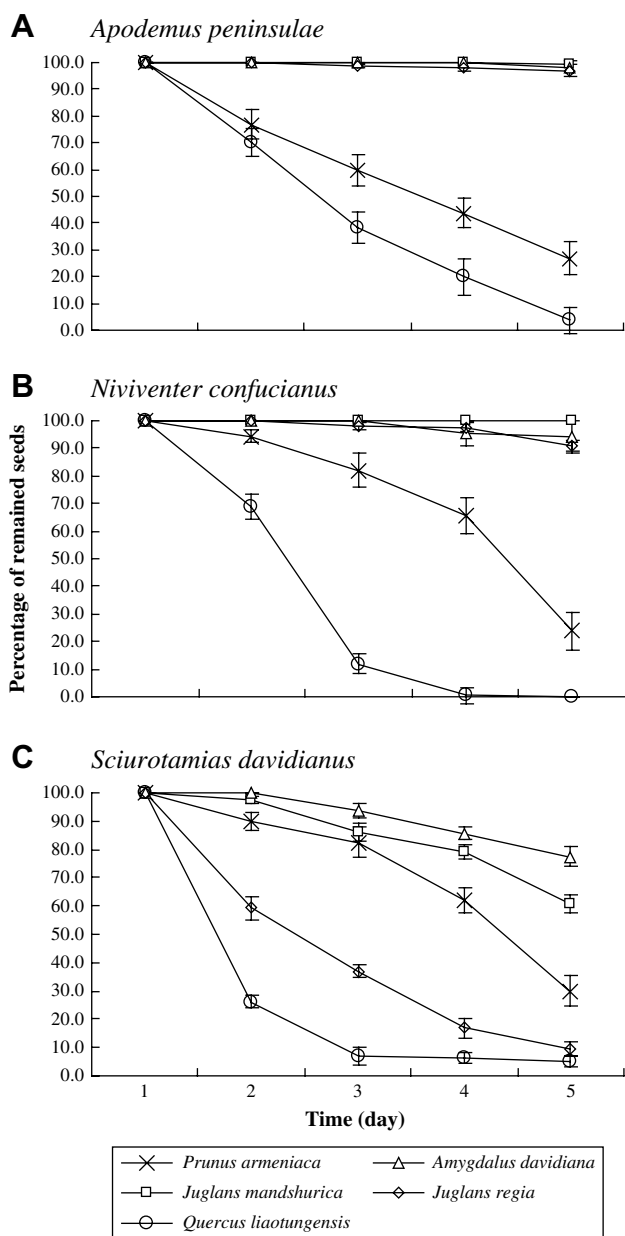
Fig. 2 – Seed selection by the three rodent species in cage experiments. Error bars are standard errors.

and the heaviest masseter, consumed all of the five seed species regardless of seed size and endocarp thickness. However, Price (1983) found six heteromyid rodent species with different body size to have similar preferences for wheat particles of various sizes.

Levey (1987) suggested that body size is the predominant factor in determining fruit size selection by frugivorous birds. This is because the maximum diameter of fruit and/or seed swallowed by avian frugivores is mostly limited by their gape size. In contrast, there is no upper size constraint for mammalian granivores, as they are able to process fruit using their teeth and hands. The fruit-size hypothesis may not be applicable to the case of rodent selection of seeds of varying size. However, seed mass may be also a factor constraining decisions by rodents to remove and cache seeds. Small

rodents may have difficulty in handling and carrying heavy (often large) seeds, and thus suffer high predation risk. The husking time for four kinds of seeds (spinach, sunflower, squash and pumpkin) by seven species of heteromyid rodents varying in size from 8 to 114 g was inversely proportional to the animal's body size (Rosenzweig and Sterner, 1970). Seeds of *J. regia* and *J. mandshurica* are over 10–20% of the body mass of *A. peninsulae* and *N. confucianus*, but less than 5% of the body mass of *S. davidianus*. The seed mass hypothesis is likely to explain why large rodents consume both small and large seeds, while small rodents select only small seeds.

4.4. Effects of seed traits on seed removal speed

The use by rodents of seeds of a given species may depend not only on traits of the rodent species but also on traits (both physical and chemical traits) of seeds. Our results clearly indicated that endocarp thickness was the principal determinant of the order of removal of seeds of the five species and supported our hypothesis. Speed of seed removal was negatively correlated with endocarp thickness. This phenomenon has also been reported by a very few other studies (e.g. Blate et al., 1998; Izhaki, 2002). This is probably because thick and hard endocarps would generally be rejected by seed predators owing to the difficulty of handling them or to the high energy expenditure or high predation risk this would entail. Very large, physically well-protected seeds often suffer almost no predation (Terborgh et al., 1993; Blate et al., 1998; Kollmann et al., 1998). For seed predators, decisions concerning where and what to eat depend on the trade-off between handling time and predation risk (Lima and Dill, 1990). Spending more time on hard seeds may increase predation risk in the field. For instance, black-capped chickadees (*Poecile atricapillus*) changed their foraging strategy depending on predation risk, eating small, easy to handle items at unsheltered sites (Lima, 1985). In another study, seed predation by rodents was lowest among species with woody endocarps (e.g. *Cornus sanguinea*, *Crataegus* spp.) (Kollmann et al., 1998).

Seed removal speed only represents dispersal fitness of seeds by rodents before seed caching. Zhang et al. (2008) found that seed dispersal fitness might be different before seed removal and after seed removal. Though seed endocarp thickness reduced seed removal speed, it may increase seed caching after seed removal, and then increase dispersal fitness in the later stage. Our previous study indicates that both *N. confucianus* and *A. peninsulae* prefer to eat seeds of *Q. liaotungensis in situ* and to cache seeds of *P. armeniaca* in enclosure tests in the same site studied here (Lu and Zhang, 2005c,d). Ganesh and Davidar (2005) also suggested that endocarp thickness is also significant in lowering seed predation. Thus, the role of endocarp thickness in shaping interaction between seeds and animals needs further investigations by emphasizing effect of endocarp thickness on seed caching and survival after seed removal.

Our results appear contradictory to the frequent finding that larger seeds or those with higher nutritional values are removed faster than small seeds or those with low nutritional values (Brewer, 2001; Jansen et al., 2002; Vander Wall, 2003; Ulft, 2004; Xiao et al., 2004, 2005a, 2006; Celis-Diez and Bustamante, 2005). According to optimal foraging theory

(Pulliam, 1974), foragers should select a subset from the set of potential food items that maximizes net energy intake per unit time spent foraging. Rodents should forage for seeds with high value that best satisfy their nutritional demands. Many previous studies have tended to support this point of view (e.g. Lewis, 1982; Levey, 1987; Henderson, 1990). Secondary chemical compounds (e.g., tannins and other polyphenols) may also affect seed removal (e.g. Robbins et al., 1991; Dearing, 1997; Meiser et al., 2000; Burritt and Provenza, 2000; Dearing et al., 2000; Shimada and Saitoh, 2003). Tannins, a diverse group of soluble phenolic compounds, are thought to be defenses against herbivory (Robbins et al., 1991; Dearing, 1997; Meiser et al., 2000; Shimada and Saitoh, 2003). Rodents often avoid acorns with high tannin concentration (Shimada, 2001; Shimada and Saitoh, 2003). In our study, in addition to differences in endocarp thickness, there were great differences among species in seed size, nutritional value and tannin content. Of these variables, only endocarp thickness was significantly correlated with seed removal in the field. The effect of seed size, nutrition and tannin on seed removal was probably obscured by the strong effect of endocarp thickness. Kollmann et al. (1998) also found that rodent preferences for seeds of 12 fleshy-fruited species were not correlated with seed mass. Thus seeds with an endocarp that is too thick would not be favored for removal by rodents if the nutritional content were similar. For example, *P. armeniaca* and *A. davidiana* have a similar amount of caloric energy per seed, but *A. davidiana* has a much thicker endocarp than *P. armeniaca* (Table 2). *Amygdalus davidiana* was less often removed by rodents than *P. armeniaca* in both the field and the laboratory tests. However, when differences in nutritional value are much greater than those in endocarp thickness, seed size and nutrition might play a larger role in influencing seed removal probability. For example, *A. davidiana* and *J. mandshurica* have similar endocarp thickness and endocarp mass/seed mass, but *J. mandshurica* has much higher nutritional content per seed than *A. davidiana* (Table 2). *Amygdalus davidiana* is selected much less than *J. mandshurica* in both field tests and laboratory tests (for *S. davidianus*). In the seed selection experiments in cages, *S. davidianus* selected the large seeds of *J. regia* over those of *P. armeniaca*, *J.mandshurica* and *A. davidiana*, also indicating the effect of seed size and nutrition when endocarp thickness is high.

In summary, speed of seed removal was determined primarily by endocarp thickness in the temperate forest we studied. The effect on seed removal of seed size, nutritional content, and content of secondary compounds might be hidden by the strong effect of endocarp thickness. The role of the seed coat in affecting seed fates and recruitment success in tree populations, and the evolutionary significance of variation in this trait, are worthy of deeper exploration.

Acknowledgements

REFERENCES

Blate, G.M., Peart, D.R., Leighton, M., 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. Oikos 82, 522–538.

Brewer, S.W., 2001. Predation and dispersal of large and small seeds of a tropical palm. Oikos 92, 245–255.

Burritt, E.A., Provenza, F.D., 2000. Role of toxins in intake of varied diets by sheep. J. Chem. Ecol. 26, 1991–2005.

Celis-Diez, J.L., Bustamante, R.O., 2005. Frequency-dependent seed size selection on *Cryptocarya alba* (Mol.) Looser (Lauraceae): testing the effect of background. Biol. J. Linn. Soc. 84, 137–142.

Dearing, M.D., 1997. Effects of *Acomastylis rossii* tannins on a mammalian herbivore, the North American pika, *Ochotona princeps*. Oecologia 109, 122–131.

Dearing, M.D., Mangione, A.M., Karasov, W.H., 2000. Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. Oecologia 123, 397–405.

Eriksson, O., 1999. Seed size variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalia*. Acta Oecol. 20, 61–66.

Frank, C.L., 1988. The relationship of water content, seed selection, and the water requirements of a heteromyid rodent. Physiol. Zool. 61, 527–534.

Ganesh, T., Davidar, P., 2005. Fruiting phenology and pre-dispersal seed predation in a rainforest in southern Western Ghats, India. In: Dew, J.L., Boubli, J.P. (Eds.), Tropical Fruits and Frugivores: the Search for Strong Interactors. Zoological Society of San Diego, San Diego, USA, pp. 139–154.

Henderson, C.B., 1990. The influence of seed apparency, nutrient content and chemical defenses on dietary preference in *Dipodomys ordii*. Oecologia 82, 333–341.

Hulbert, A.J., Macmillen, R.E., 1988. The influence of ambient temperature, seed composition and body size on water balance and seed selection in coexisting heteromyid rodents. Oecologia 75, 521–526.

Iida, S., 1996. Quantitative analysis of acorn transportation by rodents using magnetic locator. Vegetatio 124, 39–43.

Izhaki, I., 2002. The role of fruit traits in determining fruit removal in east Mediterranean Ecosystems. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Wallingford, pp. 161–175.

Jakobsson, A., Eriksson, O., 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88, 494–502.

Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J., Van Wieren, S.E., 2002. The role of seed size in dispersal by a scatter-hoarding rodent. In: Levey, D., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal, Frugivory: Ecology, Evolution, Conservation. CABI Publishing, Wallingford, pp. 209–225.

Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. 2, 465–492.

Jenkins, S.H., 1988. Comments on relationship between native seed preferences of shrub-steppe granivores and seed nutritional characteristics. Oecologia 75, 481–482.

Jensen, S.P., 1993. Temporal changes in food preference of wood mice (*Apodemus sylvaticus* L.). Oecologia 70, 214–221.

Kaufman, L.W., Collier, G., 1981. The economics of seed handling. Am. Nat. 118, 46–60.

Kelrick, M.I., MacMzhon, J.A., 1985. Nutritional and physical attributes of seed of some common sagebrush-steppe plants: some implications for ecological theory and management. J. Range Manage 38, 65–69.

Kelrick, M.I., MacMzhon, J.A., Parmenter, R.R., Sisson, D.V., 1986. Native seed preferences of shrub steppe rodents, birds and ants: the relationship of seed attributes and seed use. Oecologia 68, 327–337.

Kerley, G.I.H., Erasmus, T., 1991. What do mice select for in seeds? Oecologia 86, 261–267.

Kollmann, J., Coomes, D.A., White, S.M., 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Funct. Ecol. 12, 683–690.

Levey, D.J., 1987. Seed size and fruit-handling techniques of avian frugiviores. Am. Nat. 129, 471–485.

Lewis, A.R., 1982. Selection of nuts by gray squirrels and optimal foraging theory. Am. Midl. Nat. 107, 250–257.

Li, H.J., Zhang, Z.B., 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). Forest Ecol. Manage 176, 387–396.

Li, H.J., Zhang, Z.B., 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). Forest Ecol. Manage. doi:10.1016/j.foreco.2007.01.063.

Lima, S.L., 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. Oecologia 66, 60–67.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lu, J.Q., Zhang, Z.B., 2004. Effects of habitat and season on removal and hoarding of seeds of wild apricot (*Prunus armeniaca*) by small rodents. Acta Oecol. 26, 247–254.

Lu, J.Q., Zhang, Z.B., 2005a. Effects of high and low shrubs on acorn hoarding and dispersal of Liaodong oak *Quercus liaotungensis* by small rodents. Acta Zool. Sinica 51, 195–204. (in Chinese with English abstract).

Lu, J.Q., Zhang, Z.B., 2005b. Food-hoarding behavior of David's rock squirrel *Sciurotamias davidianus*. Acta Zool. Sinica 51, 376–382 (in English with Chinese abstract).

Lu, J.Q., Zhang, Z.B., 2005c. Food hoarding behavior of large field mouse *Apodemus peninsulae*. Acta Theriol. 50, 51–58.

Lu, J.Q., Zhang, Z.B., 2005d. Food hoarding behavior of Chinese white-bellied rat *Niviventer confucianus*. Acta Theriol. Sinica. 25, 248–253 (In Chinese with English abstract).

Meiser, H., Hagedorn, H.W., Schulz, R., 2000. Pyrogallol poisoning of pigeons caused by acorns. Avian Dis. 44, 205–209.

Moles, A.T., Westoby, M., 2003. Latitude, seed predation and seed mass. J. Biogeogr. 30, 105–128.

Price, M.V., 1983. Laboratory studies of seed size and seed species selection by heteromyid rodents. Oecologia 60 259–236.

Pulliam, H.R., 1974. On the theory of optimal diets. Am. Nat. 108, 59–74.

Robbins, C.T., Hangerman, A.E., Austin, P.J., Mcarthur, C., Hanley, T.A., 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. J. Mammal 72, 480–486.

Rosenzweig, M.L., Sterner, P.W., 1970. Population ecology of desert rodent communities: body size and seed-husking as bases for heteromyid coexistence. Ecology 51, 217–224.

Shimada, T., 2001. Hoarding behaviors of two wood mouse species: different preference for acorns of two Fagaceae species. Ecol. Res. 16, 127–133.

Shimada, T., Saitoh, T., 2003. Negative effects of acorns on the wood mouse *Apodemus speciosus*. Popul. Ecol. 45, 7–17.

Sork, V.L., 1983. Mammalian seed dispersal of pignut hickory during three fruiting seasons. Ecology 64, 1049–1056.

Steele, M.A., Knowles, T., Bridle, K., Simms, E., 1993. Tannins and partial consumption of acorns: implications for dispersal of oaks by seed predators. Am. Midl. Nat. 130, 229–238.

Terborgh, J., Losos, E., Riley, M.P., Bolanos-Riley, M., 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. Vegetatio 107-108, 375–386.

Ulft, L.H., 2004. The effect of seed mass and gap size on seed fate of tropical rain forest tree species in Guiyana. Plant Biol. 6, 214–221.

Vander Wall, S.B., 1990. Food Hoarding in Animals. University of Chicago Press, Chicago.

Vander Wall, S.B., 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. Oikos 100, 25–34.

Vieira, E.M., Pizo, M.A., Izar, P., 2003. Fruit and seed exploitation by small rodents of the Brazilian Atlantic forest. Mammalia 67, 1–7.

Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. Forest Ecol. Manage 195, 141–150.

Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2005a. Effects of seed size on dispersal distance in five rodent-dispersed *fagaceous* species. Acta Oecol. 18, 221–229.

Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2005b. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii* (Fagaceae). Plant Ecol. 177, 249–257.

Xiao, Z.S., Wang, Y.S., Marvin, H., Zhang, Z.B., 2006. Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China. Forest Ecol. Manage 222, 46–54.

Yang, X.P., 2002. Animal Physiology. Higher Education Press, Beijing, China (in Chinese).

Zhang, H.M., Chen, Y., Zhang, Z.B., 2008. Differences of dispersal fitness of large and small acorns of Liaodong oak (*Quercus liaotungensis*) before and after seed caching by small rodents in a warm-temperate forest, China. Forest Ecol. Manage 255, 1243–1250.