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ORIGINAL ARTICLE

Differentiation in seed hoarding among three sympatric rodent species in a warm temperate forest

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Abstract

Although seed hoarding by rodents has been extensively studied, differentiation in seed-hoarding behaviors among sympatric rodent species has not been well investigated. Using semi-natural enclosures, we demonstrated that three sympatric rodent species showed clear differentiation in food selection, scatter versus larder hoarding behaviors and eating behaviors when offered seeds of four plant species from a warm temperate forest in northern China. The large field mouse *Apodemus peninsulae* preferred seeds of wild apricot (*Prunus armeniaca*) and Liaodong oak (*Quercus liaotungensis*), whereas the Chinese white-bellied rat *Niviventor confucianus* preferred seeds of cultivated walnut and Liaodong oak, and the David's rock squirrel *Sciurotamias davidianus* preferred seeds of cultivated walnut, wild apricot and Liaodong oak. All three rodents showed larder hoarding of seeds from all four plant species, but the large field mouse showed scatter hoarding of wild apricot, and the David's rock squirrel showed scatter hoarding of Liaodong oak and wild walnut. Acorns of Liaodong oak, which have a soft seed hull, were more often eaten *in situ*, whereas wild walnuts, which have a hard seed hull and more tannin, were less hoarded by all rodent species. Differentiation in the scatter versus larder hoarding behaviors of sympatric rodent species suggests that sympatric rodents play different roles in the regeneration of different sympatric plant species.

Key words: co-evolution, differentiation, larder hoarding, rodent, scatter hoarding, seed dispersal.

INTRODUCTION

Many vertebrates hoard seeds for use during periods of food shortage (Smith & Reichman 1984; Vander Wall 1990). There are two major forms of seed hoarding: larder hoarding and scatter hoarding (Smith & Reichman 1984; Hurley & Robertson 1987; Vander Wall 1990; Jenkins & Breck 1998). Seed hoarding is considered to be advantageous because it not only increases food availability during periods of scarcity, but also decreases the possibility that other foragers will find the hoarded food (Anderson & Krebs 1978; Roberts 1979; Smith & Reichman 1984; Stapanian & Smith 1984; McNamara *et al.* 1990; Brodin & Ekman 1994). The rodent families Muridae and Sciuridae are generally food hoarders, and both hoarding forms occur in species within these families (Vander Wall 1990).

Although the seed-hoarding behavior of rodents has been extensively studied by releasing tagged seeds in the field (Li & Zhang 2003; Xiao *et al.* 2003; Lu & Zhang 2004), whether different rodent species show different hoarding strategies of different seeds is not well investigated. Field

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Table 1 Treatment of the different seeds by the three rodent species

Species		Liaodong oak	Wild apricot	Cultivated walnut	Wild walnut
Apodemus peninsulae	Source	240	560	240	240
	Larder	44	35	17	2
	Scatter	0	3	0	0
Niviventor confucianus	Source	200	400	200	200
	Larder	60	7	47	5
	Scatter	0	0	0	0
Sciurotamias davidianus	Source	320	560	280	320
	Larder	0	8	32	3
	Scatter	28	0	75	0

observations that depend on the seed-releasing method are unlikely to reveal differences in seed hoarding among sympatric rodent species. Preliminary studies have suggested that sympatric rodent species might differ in their food hoarding behavior (Jenkins & Breck 1998; Price *et al.* 2000), but it is not clear whether sympatric individual rodent species have differentiated seed-hoarding behavior on different sympatric seeds. Differentiation in seed hoarding may help sympatric rodent species coexist by reducing overlapping of food niches (Jenkins & Breck 1998; Price *et al*. 2000). Revealing any differentiation in seed hoarding among sympatric rodent species may also help to understand the role of specific rodents in forest regeneration, which can help improve forest management.

In this study, we examined differentiation in hoarding behaviors of three sympatric rodent species on four different plant species in a warm temperate forest in northern China. The large field mouse *Apodemus peninsulae*, the Chinese white-bellied rat *Niviventor confucianus* and the David's rock squirrel *Sciurotamias davidianus* are dominant rodent species in the Donglingshan Mountain area of Beijing, China. The adult body weights of the David's rock squirrel, the Chinese white-bellied rat and the large field mouse are 274 g, 54 g and 24 g, respectively. Preliminary observations suggested that the three rodent species store seeds of Liaodong oak (*Quercus liaotungensis*), wild apricot (*Prunus armeniaca*), wild walnuts (*Juglans mandshurica*) and cultivated walnuts (*J. regia*) (Shou 1962; Chen *et al.* 2002; Lu 2004). Liaodong oak trees or shrubs commonly occur in this region. The acorns of Liaodong oak become ripe in autumn. Liaodong acorns weigh approximately 1.12 g each and have a soft hull. Wild apricot is the dominant shrub in the region. Wild apricot seeds weigh approximately 1.19 g each and have a very hard hull. Wild walnut trees commonly occur in the river valleys. Cultivated walnuts are planted and harvested by local farmers in the river valley. The seeds of wild and cultivated walnuts weigh approximately 6.14 g and 10.74 g, respectively, and both have a very hard hull. Seeds from these four plant species are common food items of the three rodent species. Seed-releasing experiments in the field have suggested that the seeds of these four plant species are rapidly removed and cached by rodents (Li & Zhang 2003; Lu 2004; Lu & Zhang 2004), but it is not clear how rodent species differ in scatter and larder hoarding of the four different types of seeds. The purpose of the present study was to test the hypothesis that sympatric rodent species have differentiated hoarding behaviors that vary according to the type of seed being hoarded.

Table 2 Wild apricot seed hoarding behaviors of the three sympatric rodent species

Species		Seedstatus				
		EN	B	AS	EI	ER
Apodemus peninsulae	Mean ± SD	2.50 ± 4.22	0.21 ± 0.43	0.64 ± 1.28	0	0.14 ± 0.36
(*n* = 12)	Range	0–12	0–1	0–4	0	0–1
Niviventor confucianus	Mean ± SD	0.70 ± 0.95	0	0.80 ± 0.79	0	0.10 ± 0.32
(*n* = 10)	Range	0–3	0	0–2	0	0–1
Sciurotamias davidianus	Mean ± SD	0.57 ± 0.51	0	5.21 ± 3.40	0	2.57 ± 2.50
(*n* = 14)	Range	0–1	0	1–14	0	0–9

EN, placed in the nest; B, buried in soil; AS, abandoned on the surface; EI, eaten *in situ*; ER, eaten after removal; SD, standard deviation.

Table 3 Cultivated walnut seed hoarding behaviors of the three sympatric rodent species

Species		Seed status				
		EN	B	AS	EI	ER
Apodemus peninsulae	Mean ± SD	1.42 ± 1.31	0	1.42 ± 1.31	0	0
(*n* = 12)	Range	0–4	0	0–4	0	0
Niviventor confucianus	Mean ± SD	4.70 ± 5.50	0	1.10 ± 1.20	0	0
(*n* = 10)	Range	0–18	0	0–4	0	0
Sciurotamias davidianus	Mean ± SD	2.29 ± 2.20	5.36 ± 6.78	5.00 ± 3.94	0	1.21 ± 1.48
(*n* = 14)	Range	0–6	0–18	0–14	0	0–4

EN, placed in the nest; B, buried in soil; AS, abandoned on the surface; EI, eaten *in situ*; ER, eaten after removal; SD, standard deviation.

MATERIAL AND METHODS

Study site

The study was conducted in Liyuanling village (40º00'N, 115º30'E), Mentougou District of Beijing, China, at an altitude of 1100 m a.s.l. The study area is located within the Donlingshan Mountain region and has a warm, temperate, continental monsoon climate. The local ecosystem has been severely disturbed as a result of extensive, artificial cutting and grazing by livestock over the past century. In the1990s all villagers from this area were vacated to help restore and conserve the local ecosystem. Liaodong oak, wild apricot, *Vitex negundo* and *Prunus davidiana* are common tree and shrub species. Common under-shrub species in this region include *Elymus excelsus*, *Poa* spp. and *Elsholtzia stauntoni*. Larch (*Larix principis-rupprechtii*) and Chinese pine (*Pinus tabulaeformis*) have been planted in small areas by a local reforestation farm, and walnut trees have been planted by farmers in various areas within the river valley. Wild apricots typically produce fruits from June to August, whereas cultivated walnut, wild walnut and Liaodong oak produce fruits from September to October. The large field mice, Chinese white-bellied rats and David's rock squirrels are dominant rodent species in this region (Shou 1962; Chen *et al.* 2002).

Enclosure design

Four enclosures (length × width × height = 9 m × 9 m × 1 m) were constructed on abandoned cultivated land. The enclosure walls were constructed from bricks and the inside of the walls was covered with concrete. The enclosure tops were covered with wire mesh (2.5 cm × 2.5 cm) to prevent the experimental animals escaping as well as to protect the animals from predators. The enclosure floors were cemented to prevent animals escaping by digging underground. We placed a 20-cm deep layer of soil over the bottom of the enclosure to allow the animals to hoard seeds under the soil. A wooden nest box (length × width × height = 30 cm × 20 cm × 20 cm) was placed in one corner of each enclosure. All food items were provided in a wooden feeder located in the center of each enclosure. A water bottle was placed next to each nest box. Each enclosure was divided into small quadrants to calculate the seed locations.

Experimental animals

The experimental animals were captured live from the study area. The captured animals were weighed, sexed and tagged. All experimental animals were individually housed in cages. Animals were given free access to commercial food pellets and water throughout the holding period. Lighting reflected natural day lengths during the study period from September to October 2003. Only healthy non-pregnant adults were used in the study. The mean body masses of the large field mice, Chinese white-bellied rats and David's rock squirrels used in the study were 24.29 ± 4.64 g (*n* = 12), 54.66 ± 14.94 g (*n* = 10) and 274.24 ± 18.31 g (*n* = 14), respectively.

Seed collection and marking

Seeds from wild apricot, cultivated walnut, wild walnut and Liaodong oak were used to study the hoarding behaviors of the rodents. During the fruiting periods, mature intact seeds were collected for the experiments. The fresh weight masses of the test seeds of wild apricot, Liaodong oak, cultivated walnut, and wild walnut were 1.19 ± 1.17 g

Table 4 Wild walnut seed hoarding behaviors of the three sympatric rodent species

Species		Seed status				
		EN	B	AS	EI	ER
Apodemus peninsulae	Mean ± SD	0.17 ± 0.58	0	0	0	0.17 ± 0.58
(*n* = 12)	Range	0–2	0	0	0	0–2
Niviventor confucianus	Mean ± SD	0.50 ± 0.85	0	0.60 ± 0.70	0	0
(*n* = 10)	Range	0–2	0	0–2	0	0
Sciurotamias davidianus	Mean ± SD	0.19± 0.40	0	1.19 ± 1.17	0	0.13 ± 0.34
(*n* = 14)	Range	0–1	0	0–3	0	0–1

EN, placed in the nest; B, buried in soil; AS, abandoned on the surface; EI, eaten *in situ*; ER, eaten after removal; SD, standard deviation.

(*n* = 50), 1.12 ± 0.30 g (*n* = 50) g, 10.74 ± 1.42 g (*n* = 50) and 6.14 ± 0.57 g (*n* = 50), respectively. Among these species, Liaodong oak seeds have the thinnest seed coat and cultivated walnuts are rich in nutrients. Seeds were marked following the method of Zhang and Wang (2001) and Li and Zhang (2003). Tiny holes were drilled into each seed and a small, light tin-tag (3-cm long and 1-cm wide) was connected with fine wire that was 3-cm long. The tags were coded using a sharpened metal-pen. The tags were easily seen after the animals buried the seeds because the tags remained on the ground surface. The weight of the metal tags (0.1 g) was negligible relative to the weight of the food item. The tags did not significantly change the food hoarding behavior of these rodents (Li & Zhang 2003; Xiao *et al*. 2004; Lu & Zhang 2004).

Experimental procedures

Animals showed a high tendency to hoard seeds during this period for overwintering. One animal was randomly assigned to each of the four enclosures. Animals were deprived of food for 6 h prior to being placed into the enclosures, and they were allowed to adapt to the new environment for 3 h before the seeds were provided. Only one type of seed at a time was provided for each animal, and each animal was tested only once for each type of seed. However, each animal was tested with several different types of seeds.

Forty marked seeds of wild apricot were placed in the feeder of each enclosure with each tested animal. Twenty-four hours after the animal was released into the enclosure, all tagged seeds in each enclosure were located. The status and location of each tagged seed was recorded. Seed status was classified into five categories by referring to Li and Zhang (2003): (i) eaten *in situ* (EI): the tagged seeds were eaten at or near the feeder; (ii) eaten after removal (ER): the tagged seeds were eaten on the ground surface

Table 5 Liaodong oak seed hoarding behaviors of the three sympatric rodent species

Species		Seed status				
		EN	B	AS	EI	ER
Apodemus peninsulae	Mean ± SD	3.67 ± 2.87	0	0.75 ± 0.75	0.25 ± 0.87	1.25 ± 1.71
(*n* = 12)	Range	0–10	0	0–2	0–3	0–6
Niviventor confucianus	Mean ± SD	6.00 ± 6.38	0	0.50 ± 0.71	1.00 ± 1.76	0.6 ± 1.08
(*n* = 10)	Range	0–17	0	0–2	0–5	0–3
Sciurotamias davidianus	Mean ± SD	0	0.81 ± 1.80	0.81 ± 1.33	3.44 ± 2.97	8.44 ± 3.03
(*n* = 14)	Range	0	0–7	0–5	2–8	3–12

EN, placed in the nest; B, buried in soil; AS, abandoned on the surface; EI, eaten *in situ*; ER, eaten after removal; SD, standard deviation.

Table 6 Larder versus scatter hoarding behaviors of the three sympatric rodent species of seeds from four sympatric plant species

Species	Hoarding behavior	Wild apricot	Cultivated walnuts	Liaodong oak	Wild walnuts
Apodemus	Larder	+	+	+	+
peninsulae	Scatter	+	–	–	–
Niviventor	Larder	+	+	+	+
confucianus	Scatter	–	–	–	–
Sciurotamias	Larder	+	+	+	+
davidianus	Scatter	–	+	+	–

+, selected; –, not selected.

after removal; (iii) buried in soil (B): the tagged seeds were buried in soil and they were intact; (iv) placed in the nest (EN): the tagged seeds were transported into the nest box; and (v) abandoned on the surface (AS): the tagged seeds were abandoned intact on the ground surface after removal. The total number of seeds provided from the four plant species are listed in Table 1. The study was carried out from September to October 2003.

We classified food items transported into nest boxes as larder hoarded and food items buried in the soil of the enclosures as scatter hoarded in line with previous studies (e.g. Smith & Reichman 1984; Vander Wall 1990; Jenkins & Breck 1998).

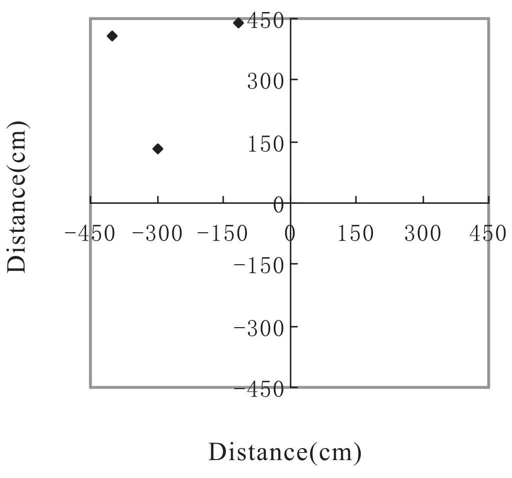

Figure 1 Scatter-hoarding pattern of wild apricot by large field mouse within enclosures.

Statistical analyses

We used SPSS for Windows (version 13.0) for the statistical analyses. Kruskal–Wallis tests were used to compare differences among the three species of rodents with respect to larder-hoarded seeds and consumed seeds.

RESULTS

Seed hoarding of wild apricot

As shown in Tables 1 and 2, all three rodent species showed larder hoarding of wild apricot seeds, but *A. peninsulae* showed both scatter and larder hoarding of wild apricot (Fig. 1). The cache size was one seed per cache and the mean transport distance of these seeds was 451. 57 ± 122.93 cm. None of the species ate the seeds of wild apricot *in situ*. *Apodemus peninsulae* tended to store more seeds in the nest boxes than the other two species, but this difference was not significant (Kruskal–Wallis test, $\chi^2 = 0.545$, d.f. = 2, $P = 0.761$). *Sciurotamias davidianus* tended to consume more seeds than the other two species (Kruskal–Wallis test, $\chi^2= 21.247$, d.f. = 2, $P = 0.000$).

Seed hoarding of cultivated walnuts

As shown in Table 3, all three species showed larder hoarding of cultivated walnuts, but only *S. davidianus* showed both scatter and larder hoarding of cultivated walnuts (Fig. 2). None of the species ate cultivated walnut seeds *in situ*. *Niviventor confucianus* tended to store more seeds in the nest boxes than the other two species, but this difference was not significant (Kruskal–Wallis test, $\chi^2 = 1.984$, d.f. = 2, $P = 0.371$). The cache size was one seed per cache and the mean transport distance of these nuts was 435.30 ± 114.82 cm. Only David's rock squirrels were observed to eat walnuts away from the feeders.

Seed hoarding of wild walnuts

As shown in Table 4, all three species showed larder hoarding of wild walnuts, and no species showed scatter hoarding of wild walnuts. None of the species ate the seeds of wild walnuts *in situ*.

Seed hoarding of Liaodong oak

As shown in Table 5, only *A. peninsulae* and *N. confucianus* showed a high tendency to larder hoard Liaodong oak, and only *S. davidianus* showed scatter hoarding of Liaodong oak. The cache size was one acorn per cache, and the mean transport distance of these acorns was 275.87 ± 163.20 cm. *Sciurotamias davidianus* ate more

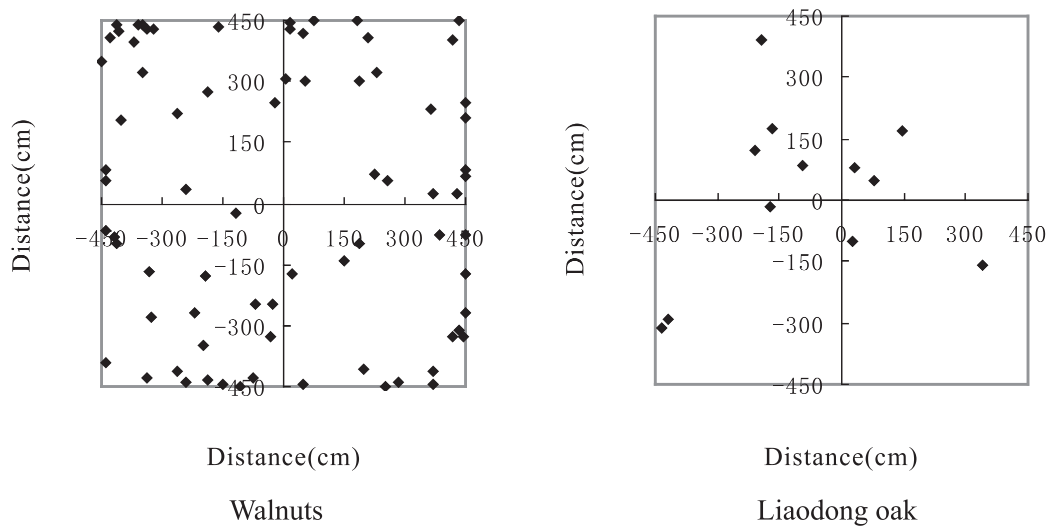

Figure 2 Scatter-hoarding pattern of (a) walnuts and (b) acorns of Liaodong oak by David's rock squirrels within enclosures.

acorns of Liaodong oak than the other two species *in situ* (Kruskal–Wallis test, $\chi^2 = 13.100$, d.f. = 2, $P = 0.001$) and after removal (Kruskal–Wallis test, $\chi^2 = 27.234$, d.f. = 2, $P = 0.000$). All rodent species ate acorns of Liaodong oak *in situ*.

Niviventor confucianus ate more acorns of Laiodong oak inside the nest boxes than the other two species (Kruskal–Wallis test, $\chi^2 = 23.291$, d.f. = 2, $P = 0.000$).

The scatter-hoarding versus larder-hoarding strategies of these three sympatric rodent species are summarized in Table 6. All rodent species showed larder-hoarding behaviors of the four seed types, but only the large field mice showed scatter-hoarding behavior of seeds of wild apricot, and only David's rock squirrels showed scatter-hoarding behavior of seeds of Liaodong oak and cultivated walnuts.

DISCUSSION

Our study demonstrated that the three sympatric rodent species showed clear differentiation in food selection, scatter versus larder-hoarding behaviors, and eating behaviors of seeds from four species. *Apodemus peninsulae* preferred to hoard or eat seeds of wild apricot and Liaodong oak. This species showed larder-hoarding behavior of all four plant species, but only showed scatter hoarding of wild apricot. *Apodemus peninsulae* only ate seeds of Liaodong oak *in situ*. *Niviventor confucianus* preferred to hoard or eat the seeds of cultivated walnuts and Liaodong oak. This species showed larder-hoarding behavior of all four plant species, but no scatter-hoarding behavior. *Niviventor confucianus* only ate acorns of Liaodong oak *in situ*. *Sciurotamias davidianus* preferred to hoard or eat seeds of cultivated walnuts, wild apricot and Liaodong oak. This species showed larder-hoarding behavior of all four plant species, but only showed scatter-hoarding of seeds of cultivated walnuts and Liaodong oak. *Sciurotamias davidianus* only ate acorns of Liaodong oak *in situ*.

The coexistence of ecologically similar rodent species has been a subject of interests for decades (Randall 1993; Leaver & Daly 2001). However, community ecologists have largely ignored the role of food hoarding in the competition and coexistence of rodents. It is generally thought that mechanisms of coexistence arise when there are trade-offs among species in their ability to use resources along an axis of resource heterogeneity that is caused by environmental factors (Kotler & Brown 1988). Heterogeneity among species in their strategies for harvesting and hoarding seeds has the potential to promote coexistence (Price *et al*. 2000; Vander Wall 2000; Leaver & Daly 2001). Differentiation in the three sympatric rodent species in food selection, hoarding and consumption behaviors may contribute to their coexistence in the study region.

Mutualism between plants and dispersers is believed to be diffuse because one plant species may depend on many dispersers, and one disperser species may rely on many plant species. Co-evolution between plants and their dispersers is likely to be diffuse rather than species specific (Herrera 1985). Our study indicates that the scatter-hoarding relationship tends to be more species specific than previously thought. We did not find any overlapping of scatter-hoarding rodents with regard to seed type. Each plant species had only one rodent species that scatter hoarded its seeds. However, one rodent species may show scatter hoarding of more that one plant species (e.g. David's rock squirrel). Because scatter-hoarding rodents may have a better chance of re-locating buried seeds, the specific link between a plant and its scatter-hoarding rodent species would promote the formation of more specific co-evolution.

A number of prior studies have shown two types of food hoarding in rodent species similar to those examined in the present study, for example, *Tamias striatus* (Clarke & Kramer 1994), *Peromyscus maniculatus* (Vander Wall *et al.* 2001) and *Dipodomys merriami* (Preston & Jacobs 2001). Several studies support the idea that rodents use different hoarding patterns in relation to the characteristics of the habitat, and that animals that inhabit desert areas prefer to eat food with a high carbohydrate content that is low in protein in relation to water economy (Lockard & Lockard 1971; Price 1983; Kelrick *et al.* 1986; Frank 1988). It is hypothesized that a dual storage strategy may enhance the ability of these species to survive long winters when available food is scarce. Larder hoarding permits them to guard some food from pilfering, and scatter hoarding provides potential resources if their nest is overtaken or destroyed. This hypothesis does not explain why some rodents show both hoarding behaviors of the same plant species, while only showing one hoarding behavior of another plant species. A hoarder's ability to defend stored food may influence their choice in hoarding strategy (Morris 1962; MacDonald 1976; Smith & Reichman 1984; Vander Wall 1990; Jenkins & Breck 1998; Stelis 2000; Vander Wall & Jenkins 2002). Inter-species dominance status was generally correlated with larger body size (Jenkins & Breck 1998; Vander Wall 1990; Smulders 1998; Price *et al.* 2000). Thus, larger animal species are more capable of defending stored foods and may tend to show larder hoarding and vice versa (Jenkins & Breck 1998; Smulders 1998; Price *et al.* 2000). This hypothesis does not appear to be supported by our observation that both large rodent species (David's rock squirrel) and small rodent species (large field mouse) show scatter-hoarding and larder-hoarding behaviors.

The specific characteristics of the food items affect the hoarding strategy of rodents (Tamura *et al.* 1999). How an animal responds to a food item can be affected by the ease with which it can be immediately consumed (Jacobs 1992) as well as its storage potential (Reichman 1988; Vander Wall 1990, 1995; Post & Reichman 1991; Jacobs 1992). Animals are reported to restrict feeding in areas where feeding activities increase predation risk (Jacobs 1992; Clarke & Kramer 1994; Lima 1998). Seeds with hard hulls are more likely to be cached instead of being eaten *in situ* (Zhang *et al.* 2005) than seeds with soft hulls, probably because eating hard seeds *in situ* needs longer handling time increasing the risk of exposure to predators. Hurley and Roberston (1987) relate the storage strategy to the value of the food "and to the cost of loss by theft by conspecifics or other species". These authors suggested that the largest food items (i.e. more "valuable") are stored in a more disperse manner to reduce the likelihood of their being stolen. In the present study, all Liaodong oak acorns, which have thin and soft seed hulls, were eaten *in situ* by all three rodent species. Acorns of Liaodong oak were hoarded less by *S. davidianus* and *A. peninsulae*, probably because they had low potential storage value because of the acorn's relative low nutrition and propensity for insect infestation. Prior studies have shown that the percentage of acorns at a study site that are infested with weevils can be as high as 45.4% (Yu *et al.* 2001). Acorns of Liaodong oak rapidly deteriorate when infected by insects (Sun & Chen 2000; Steele *et al*. 1996). In contrast, cultivated walnuts were more likely to be cached by *S. davidianus* and *N. confucianus*, probably because they had hard hulls and high nutrition values. Wild walnuts seem to be less selected by all rodents, although the seed mass and seed hull are similar to the cultivated walnuts. This is probably because wild walnuts contain less nutrition and higher levels of tannin than cultivated walnuts. Leaver and Daly (1998) found that *Dipodomys merriami* (Heteromyidae) stored proportionately more food rich in carbohydrates, and related these results to food preference.

A small proportion of scatter-hoarded seeds may recruit seedlings under favorable conditions (Vander Wall 1990; Forget & Vander Wall 2001; Li & Zhang 2003; Xiao *et al*. 2004; Lu & Zhang 2004). Thus, rodents exhibiting scatter-hoarding behavior would benefit the forest regeneration of specific tree species; whereas rodents only showing larder-hoarding behavior would contribute little to forest regeneration. In the present study, *N. confucianus* showed no scatter hoarding of seeds of any plant species and, thus, made little positive contribution to forest regeneration. *Sciurotamias davidianus* made an important positive contribution to the regeneration of Liaodong oak and cultivated walnut, but little positive contribution to the regeneration of wild walnut and wild apricot.

Apodemus peninsulae made an important positive contribution to the regeneration of wild walnut, but little positive contribution to Liaodong oak, wild walnuts and cultivated walnuts. Thus, differentiation in scatter versus larder hoarding among sympatric rodent species suggests that sympatric rodents play different roles in the regeneration of different sympatric plants.

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