Seed consumption and caching on seeds of three sympatric tree species by four sympatric rodent species in a subtropical forest, China

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Abstract

Because it is difficult and often impossible to distinguish dispersal, consumption and caching of seeds among different rodent species in the field, the differences of sympatric rodent species in affecting seed fates and forest regeneration are often unknown. To understand the different impact of four sympatric rodent species on seed fates of three sympatric tree species, we studied the food-hoarding behavior of Edward's long-tailed rats (*Leopoldamys edwardsi*), Chestnut rats (*Niviventer fulvescens*), Himalayan rats (*Rattus nitidus*) and Norway rats (*R. norvegicus*) on seeds of three sympatric tree species: Cork oak (*Quercus variabilis*), Serrate oak (*Q. serrata*) and Oil tea (*Camellia oleifera*) in a subtropical forest in the Dujiangyan Region, Sichuan Province, China. Consumption and caching of tagged seeds by rodents was measured in enclosures (10 m × 10 m) from September to December 2003. The results showed that Edward's long-tailed rats scatter-hoarded seeds of the three tree species. They scatter-hoarded Serrate oak significantly less than Cork oak (with large seed size) and Oil tea (with high energy). The transport distances of Serrate oak by all the four rodent species were significantly shorter than those of Cork oak and Oil tea. The cache sizes of the three seed species were all small. Most seeds were cached under grass or shrubs in the enclosure. In terms of the population abundance and food preference, Edward's long-tailed rats imposed most and the largest impact on seed fate of the three tree species. The results supported our hypothesis that sympatric rodent species may affect seed fate and forest regeneration differently. Only Edward's long-tailed rats might benefit the seed recruitment of Cork oak, Serrate oak and Oil tea, while the other three rodent species were purely seed-eater and thus might contribute little to seed regeneration of the three dominant tree species.

1. Introduction

Seed-caching rodents are well known as both seed dispersers by burying seeds in the soil and seed predators by consuming large quantities of seed crops

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in forest ecosystems (Vander Wall, 1990, 2001; Forget et al., 1998; Zhang and Wang, 2001a; Jansen et al., 2002). Seed-hoarding may benefit plants by reducing the probability of predation by other predators and increasing the probability of seedling establishment. Rodents play an important role in the ecology and evolution of plants if their patterns of activity influence subsequent stages of the plant life cycle (Willson and Traveset, 2000; Wang and Smith, 2002).

By tracing tagged seeds or by using alternative methods, seed dispersal and seed caching have been extensively studied in the field (Hutchins et al., 1996; Kollmann and Schill, 1996; Hurly and Lourie, 1997; Silva and Tabarelli, 2001). Because it is difficult and often impossible to distinguish dispersal, consumption and caching of seeds among different rodent species in the field, the differences of sympatric rodent species in affecting seed fates and forest regeneration are often unknown (Jansen et al., 2002). To understand the impact of sympatric rodents on seed fates of different sympatric seeds, we need resort to enclosure experiments through manipulating animals and seeds. Several studies have been conducted to study seed-hoarding in enclosures (e.g., Jenkins and Peters, 1992; Jenkins et al., 1995; Jenkins and Breck, 1998; Price et al., 2000; Shimada, 2001; Hollander and Vander Wall, 2004), but few studies deal with food-hoarding with multiple species interactions among sympatric rodent species and seeds of sympatric trees.

The characteristics of both seeds and rodents may influence seed predation and hoarding by rodents. Food abundance (Alm et al., 2002), seed size (Garb et al., 2000; Ivan and Swihart, 2000), hardness of seed hull (Sako et al., 2002), perishability (Post and Reichman, 1991; Hadj-Chikh et al., 1996), palatability or nutrient composition (Laska et al., 2003), secondary compounds (Dixon and Johnson, 1997), seed energetic value (Lewis et al., 2001) are important factors in influencing seed predation and hoarding by rodents. Body size, age, sex, social structure, food preference and predator avoidance of rodents (Kitchen et al., 1999; Arjo et al., 2002; Taraborelli et al., 2003; Vander Wall and Jenkins, 2003) are also important factors in influencing seed predation and hoarding by rodents.

Competition theory predicts that potential competitors coexisting in a community should exhibit niche differentiation or resource partitioning to avoid competition (Begon et al., 1986). Food, habitat and time have been suggested to be the most important niche dimensions in resource partitioning between species (Schoener, 1986). Among the three factors, food is the most important factor in resource partition between sympatric species. It is currently believed that food niche partitioning is the principal factor allowing coexistence of sympatric species in rodents (Kronfeld-Schor and Dayan, 1999). Jenkins and Breck (1998) suggested that differences in hoarding behavior among species might facilitate coexistence. At present, it is generally thought rodent affect seed fates of forest as a 'guild', it is not clear whether sympatric rodent species differ in seed-hoarding behaviors (especially scatter-hoarding versus larder hoarding). Lu and Zhang (2004a) found though several sympatric rodent species consumed seeds of wild apricot (*Prunus armeniaca*) in a warm temperate forest of China, but only large field mouse (*Apodemus peinsulae*) was found to scatter-hoard seeds of wild apricot based on comparing dental marks of different rodents on the hard seed hulls. We hypothesize that sympatric rodent species may differentiate in hoarding seeds of sympatric tree species, and thus these sympatric rodent species may play different roles in seed regeneration of these sympatric tree species.

In a subtropical evergreen broadleaved forest in Dujiangyan Region of Sichuan Province, China, at least 10 rodent species coexist: Edward's long-tailed rats (*Leopoldamys edwardsi*), Bower's rats (*Berylmys bowersi*), Chestnut rats (*Niviventer fulvescens*), Himalayan rats (*Rattus nitidus*), Norway rats (*R. norvegicus*), Chinese white-bellied rats (*N. confucianus*), Sichuan field mice (*Apodemus latronum*), Chevrier's field mice (*A. chevrieri*), South China field mice (*A. draco*) and Harvest mice (*Micromys minutus*) (Xiao et al., 2002). Field studies indicated that these rodents consumed the seeds of Cork oak (*Quercus varialilis*), Serrate oak (*Q. Serrata*), *Lithocarpus harlandii*, *Cyclobalanopsis glauca*, *Castanopsis fargesii* and Oil tea (*Camellia oleifera*) (Xiao and Zhang, 2004). By using semi-natural enclosures, this study aims to test if four dominant sympatric rodent species (Edward's long-tailed rats, Chestnut rats, Himalayan rats and Norway rats) differ in hoarding seeds of three dominant sympatric tree species (Cork oak, Serrate oak and Oil tea) in the Dujiangyan Region of Sichuan Province, China.

2. Material and methods

2.1. Study area

The study was conducted in an experimental forest (altitude 700–1000 m, 31°4′N, 103°43′E) in the Dujiangyan Region, Sichuan Province, China, during September–October 2003. The site lies in the middle subtropical zone, with a mean annual temperature of 15.2 °C, and an annual precipitation of 1200–1800 mm (Chen, 2000). The weather is often cloudy and foggy, with only 800–1000 mean annual sunny hours and with a mean annual relative humidity of more than 80%.

2.2. Rodents

Rodents were collected using live-traps baited with peanuts. Trapping was conducted at 15 plots and each plot for consecutive five days. Each trapping grid consisted of 5×4 traps (sometimes 5×2 traps) spaced 10 m apart. Live trapping was conducted during August–October 2003 at the study site. The weights of all rodents were recorded on capture. Edward's long-tailed rats, Chestnut rats, Himalayan rats, Norway rats are the top four dominant rodent species in the study area. Two indices were used to measure population abundances of rodents: trap success and trap biomass. The trap success was defined as:

Trap success

$$= \frac{\text{total number of captured individual}}{\text{total number of traps}} \times 100\%$$

And the trap biomass was defined as:

Trap biomass

$$= \frac{\text{total biomass of captured individuals}}{\text{total number of traps}}.$$

Only adult rodents were selected as subjects in our experiment ($\geq$350 g for Edward's long-tailed rats, $\geq$60 g for Chestnut rats, $\geq$100 g for Himalayan rats and $\geq$100 g for Norway rats). Twenty-four Edward's long-tailed rats (11 males, 13 females) (mean weights $\pm$ S.D. are 427.24 ± 46.11 g), 16 Chestnut rats (9 males, 7 females) (73.03 ± 12.32 g), 8 Himalayan rats (5 males, 3 females) (164.59 ± 33.46 g) and 11 Norway rats (5 males, 6 females) (189.47 ± 44.57 g) were used in the experiment. The rodents were kept in individual cages (40 cm $\times$ 30 cm $\times$ 25 cm or 30 cm $\times$ 25 cm $\times$ 20 cm, adjusted according to body size) with sawdust substrate and dry straw as nest material. Mouse chow and water were provided for rats ad lib. Each species were separated and an 11-h light:13-h dark photoperiod was maintained.

2.3. Seeds collection and preparation

Seeds of Cork oak, Serrate oak and Oil tea in the study site were used in the experiment. The seed characteristics of the three tree species are shown in Table 1 (Xiao et al., 2003). All seeds were collected from the ground in September and October 2003 after they were mature, and only sound seeds were used in this study. We labeled the seeds using the tin-tagging method proposed by Zhang and Wang (2001a) for tracking seeds. A tiny hole 0.5 mm in diameter is drilled near the germinal disc of each seed. Though the cotyledon is partly damaged, the embryo remains intact and is capable of germinating. A small, light tin-tag (4 cm $\times$ 1 cm, <0.1 g) is tied through the hole in each seed using an 8 cm thin steel thread. Each tag is coded using a fine point metal-pen with a serial number to make each seed identifiable. When rodents bury the tagged seeds in the soil (usually <3 cm in depth), the tin-tags are often left on the surface, making them easy to relocate. The

Table 1
Seed characteristics of three tree species (Xiao et al., 2003)

Plant species	Diameter[a] (cm)	Length[a] (cm)	Fresh weight[a] (g/seed)	Crude protein (%)	Crude fat (%)	Crude starch (%)	Tannin (%)	Caloric value (J./g)
Cork oak	1.40 ± 0.15	1.88 ± 0.22	2.42 ± 0.60	5.92	3.94	54.17	11.68	17.63
Serrate oak	0.92 ± 0.11	1.77 ± 0.24	0.97 ± 0.26	6.07	3.02	54.01	10.62	17.2886
Oil tea	1.18 ± 0.27	1.51 ± 0.22	0.87 ± 0.34	10.91	51.79	11.74	0.10	29.5587

[a] Mean $\pm$ S.D., $n = 40$.

tin-tagging method had been proved to be reliable in tracing the seed fates of several tree species (Li and Zhang, 2003; Xiao et al., 2004a,b; Zhang et al., 2005). Tin-tagging had a negligible effect on seed removal and caching by rodents (Zhang and Wang, 2001a; Xiao et al., 2004a,b). Each tagged seed was weighed by an electronic scale with an accurate of ±0.1 g before these seeds were released into the enclosure.

2.4. Experiment design

The experiment was conducted in four 10 m × 10 m semi-natural enclosures simultaneously. The enclosures were built with bricks, the walls of the enclosures extended 1.5 m above and 0.5 m below ground. The walls were smoothed and the tops of enclosure were covered with a piece of large plastic cloth supported by steel frame. These measures effectively prevented subjects from escaping and predators from entering the enclosures. A layer of sand about 5–8 cm thick was covered in the enclosure to simulate soft soil in the forest. The sand was watered periodically to hold the sand as wet as soil in the forest. The habitat in the enclosures was similar and typical of the study area, consisting of a variety of shrubs and herbaceous plants (but without trees). The plant distributions in four enclosures were similar and the areas of plants in each enclosure were all about 15 m². A nest box (18 cm × 18 cm × 40 cm) with some dry straw in it was placed at the corner of each enclosure. Almost all the rats used the box as their nest during the experiment.

The experiment was conducted from September to December 2003. Several days before the experiment, the subjects were fed with the three species of seeds so that they can be familiar with them. Ten coded tin-tagged seeds of Cork oak, 20 coded tin-tagged seeds of Serrate oak and 20 coded tin-tagged seeds of Oil tea were placed on the ground in the center of each enclosure at 16:30 to 17:30. The total weight of seeds of each species place in each enclosure was adjusted to be about 20 g. This amount of seeds of the tested tree species was proved to satisfy daily demand of the tested rodent species. The subject was introduced into the enclosure and was allowed to move freely for one night. The next morning, we removed the subject, and relocated all seeds or their fragments we released in

the enclosure, and recorded their position and their states. All the cached or unharvested seeds and fragments of seeds were removed and collected at the end of the searching process. We measured weight of seeds consumed for each tree species by subtracting weight of seed fragment from original weights of these eaten seeds when they were placed in the enclosure.

Four categories of the seed-states were defined for seeds or their fragments with a small modification of the categories defined by Zhang and Wang (2001a) and Li and Zhang (2003): (1) eaten (E)—the seed was gnawed open by subject and the entire or most part of kernel was eaten by the subject; (2) buried (B)—the seed was intact and buried in soil; (3) transported but left intact on the surface (IS)—the seed was transported away from the release site but left on the surface of the ground without being eaten or cached; (4) remained and untouched (R)—the seed remained at the release site untouched.

Microhabitats of seeds of different states were also recorded. According to Li and Zhang (2003), three categories of the microhabitats were defined as: (1) naked ground (NG)—the seed or its fragment was found at the naked place without vegetation in the enclosures; (2) near the wall (NW)—the seed or its fragment was found within 30 cm of the wall of the enclosure; (3) under grass or shrubs (UGS)—the seed or its fragment was found under grass or shrubs in the enclosures.

The four rodent species differed in body weights, and the weights of seeds consumed by them also differed significantly. To compare differences in seed consumption preference among rodent species, seed consumption index (SCI) was used:

Seed consumption index (SCI)

$$= \frac{\text{seed weight consumed}}{\text{rodent body weight}} \times 100$$

In order to compare differences of impact on the three tree species among rodent species, we defined the estimated total amount of seed predation of rodents as:

The estimated total amount of seed predation

$$= \text{seed consumption index (SCI)} \times \text{trap biomass.}$$

3. Statistics

SPSS 10.0 for Windows software was used for all statistical analyses. Since the numbers of seeds categorized as IS were too small, they were not included in the analyses. Friedman tests were used to compare food preferences among the seeds of three species within each rat species. Friedman tests were also used to compare caching of the three species of seeds by Edward's long-tailed rats. Chi-square test was used to test difference in cache size of seeds among the three tree species. Kruskal–Wallis test was used to test the difference in transport distances of eaten or cached seeds among seed species within each rodent species or among rodent species within each seed species. Chi-square test was used to compare the microhabitat selection of seed cached by scattered hoarding rodents with the natural condition of microhabitat in enclosure.

4. Results

4.1. Population abundance

We only captured four species of rodents: Edward's long-tailed rats, Chestnut rats, Himalayan rats, Norway rats. We used two indices to describe population abundance of small rodents in the study area. For both indices of trap success and trap biomass, Edward's long-tailed rats were the most dominant rodent species (Fig. 1). The trap success of Edward's long-tailed rats (about 6%) was much higher than the other three rodent species (only 1.27% for Chestnut rats and both less than 1% for both Himalayan rats and Norway rats). Trap biomass of Edward's long-tailed rats made up 82.8% of the trap biomass of all rodents captured in this study.

Fig. 2. Seed consumption index (SCI) (mean ± 1S.E.) of seeds consumed by the four rodent species. Seed consumption index was get by dividing multiplication of seed weight consumed times 100 g by rodent body weight. ER: Edward's long-tailed rats ($n = 24$). CR: Chestnut rats ($n = 16$). HR: Himalayan rats ($n = 8$). NR: Norway rats ($n = 11$).

4.2. Seeds consumption, hoarding and predation pressure

The seed consumption index of rodents represents food preference of rodents for seeds tested. Edward's long-tailed rats consumed more seeds in total than the other three rodent species (Chestnut rats, Himalayan rats and Norway rats). Norway rats consumed very little seeds (Fig. 2).

There were no significant differences in seed consumption among three tree species (Cork oak, Serrate oak, Oil tea) by Edward's long-tailed rats ($\chi^2 = 0.083$, d.f. = 2, $p = 0.959$) and by Himalayan rats ($\chi^2 = 4.467$, d.f. = 2, $p = 0.107$). However, there were significant differences in seed consumption among three tree species by Chestnut rats ($\chi^2 = 13.265$, d.f. = 2, $p = 0.001$) and Norway rats ($\chi^2 = 11.371$, d.f. = 2, $p = 0.003$) (Fig. 2). Chestnut rats ate more seeds of Serrate oak and Oil tea than seeds of Cork
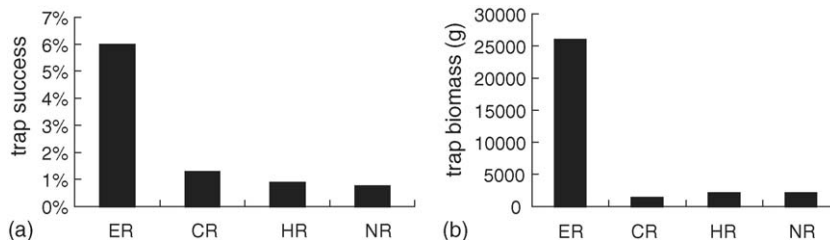

Fig. 1. Trap success (a) and trap biomass (b) of four rodent species in 2003 in Dujiangyan Region. ER: Edward's long-tailed rats. CR: Chestnut rats. HR: Himalayan rats. NR: Norway rats.
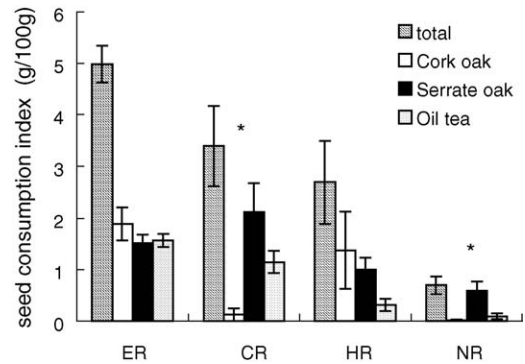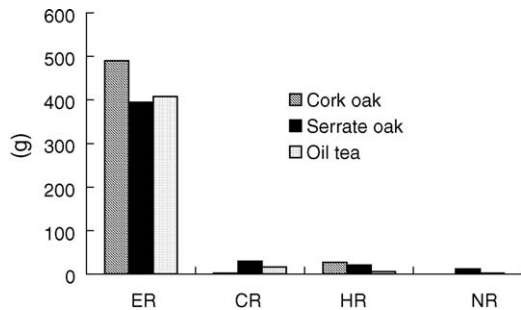
Fig. 3. Estimated total amount of seed predation on seeds of the three tree species by the four rodent species imposed in study area. estimated total amount of seed predation on seed by rodent was get by seed consumption index (SCI) × trap biomass. ER: Edward's long-tailed rats. CR: Chestnut rats. HR: Himalayan rats. NR: Norway rats.

oak. Himalayan rats ate more seeds of Cork oak and Serrate oak than seeds of Oil tea. Norway rats ate more seeds of Serrate oak than seeds of the other two tree species (Fig. 2). Only one Chestnut rat and one Norway rats were observed to eat one Cork oak.

Edward's long-tailed rats imposed high predation pressure on seeds of all the three tree species (Fig. 3). The other three rodent species imposed little. The estimated total amount of seed predation by Edward's long-tailed rats on Cork oak was a little higher than they did on Serrate oak or Oil tea. Chestnut rats imposed little predation pressure on Cork oak. Norway rats almost only imposed predation pressure on Serrate oak, they imposed little predation pressure on Cork oak or Oil tea (Fig. 3).

No Himalayan rat or Norway rat cached any seed through our experiment, neither did they scatter-hoarding nor larder-hoarding any seed. Only 1 of the 16 Chestnut rats scatter-hoarded one Oil tea, and they did not larder-hoard any seed. Edward's long-tailed rats scatter-hoarded large amount of seeds of the three tree species, but did not larder-hoard any seed. Edward's long-tailed rats cached Oil tea the most, and Serrate oak the least (Fig. 4). The difference in seed cached by Edward's long-tailed rats among the three seed species was significant ($\chi^2 = 26.271$, d.f. = 2, $p < 0.001$).

4.3. Cache size

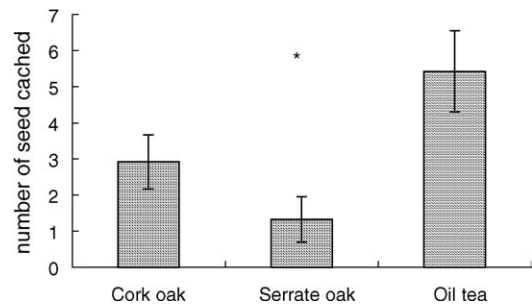Most seeds were cached individually in each cache in our experiment. The largest cache size in our

Fig. 4. The mean number (mean ± 1S.E.) of seed cached by Edward's long-tailed rats one night in the enclosure ($n = 24$).

experiment was 6, and there was only one observation of oil tea. The second largest cache size was 3, and also there was only one observation of Cork oak. There were several cache sites of all the three seed species whose cache size were 2. The frequency distribution of cache size of Cork oak, Serrate oak, Oil tea were shown in Fig. 5. There were no significant difference in cache size among the three seeds species ($\chi^2 = 5.042$, d.f. = 6, $p = 0.538$).

4.4. Transport distance

A two-way ANOVA of all the eaten seeds using rodent species and seed species as factors found that transport distances differed significantly (rodent species: $F_{3,938} = 10.186$, $p < 0.001$; seed species: $F_{2,938} = 6.233$, $p = 0.002$). Seed transport distances were greatest by Edward's long-tailed rats (mean ± S.E., 239.191 ± 9.507 cm, $n = 684$) and was least by Himalayan rats (49.192 ± 23.756 cm, $n = 114$). Seeds of Cork oak were transported the farthest (226.313 ± 82.10 cm, $n = 143$) and seeds of Serrate
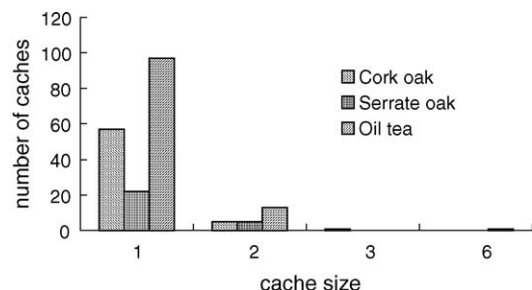

Fig. 5. Frequency distribution of cache size by Edward's long-tailed rats on Cork oak, Serrate oak and Oil tea seeds.
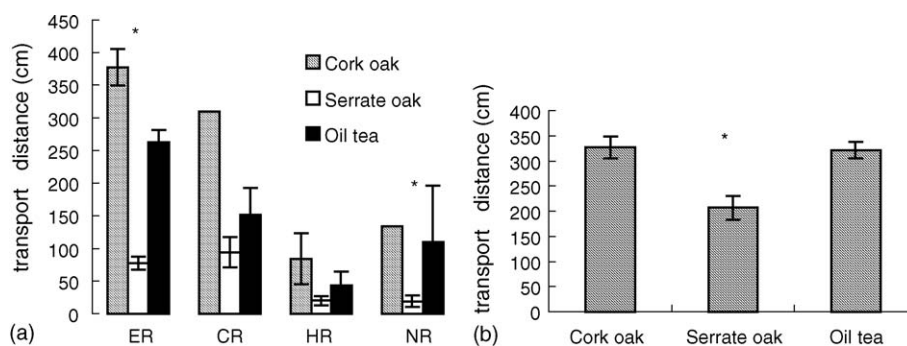
Fig. 6. Transport distances (mean ± 1S.E.) of seeds eaten by the four rodent species (a) or buried by the Edward's long-tailed rats (b). ER: Edward's long-tailed rats. CR: Chestnut rats. HR: Himalayan rats. NR: Norway rats. Sample size: (a) Cork oak by ER (120), Serrate oak by ER (312), Oil tea by ER (252), Cork oak by CR (1), Serrate oak by CR (54), Oil tea by CR (27), Cork oak by HR (21), Serrate oak by HR (63), Oil tea by HR (30), Cork oak by NR (1), Serrate oak by NR (62), Oil tea by NR (7); (b) Cork oak (70), Serrate oak (32), Oil tea (129).

oak were transported the nearest (52.642 ± 13.272 cm, $n = 491$) (Fig. 6a). There was a significant rodent species × seed species interaction ($F_{6,938} = 3.703$, $p = 0.001$), indicating that transport distance of different seed species were significant influenced by rodent species.

The results of transport distance of the three seed species cached by Edward's long-tailed rats were similar to those of seeds eaten by Edward's long-tailed rats. Edward's long-tailed rats transported seeds of Cork oak and Oil tea farther than seeds of Serrate oak (Fig. 6b). One-way ANOVA test showed that there was significant difference of transport distances of seeds among the three tree species cached by Edward's long-tailed rats ($F_{2,230} = 5.995$, $p = 0.003$).

4.5. Microhabitat of seeds being eaten or cached

In each enclosure, the proportion of microhabitat area that was near the wall was 11.64% (11.64 m^2). The proportion of microhabitat area that was under grass or shrubs was 15% (about 15 m^2). The proportion of microhabitat area that was naked ground was 73.4% (about 73.4 m^2).

The results of the Chi-square test indicated that microhabitat selection of seed consumed of the three tree species by the four rodent species all differed significantly from the natural condition of microhabitat in the enclosure ($p < 0.001$ in all test). Edward's long-tailed rats preferred eating Cork oak and Oil tea near the wall to on naked ground (Fig. 7a). Chestnut rats preferred eating Serrate oak and Oil tea under grass or

shrubs (Fig. 7b). Himalayan rats preferred eating Cork oak and Oil tea under grass or shrubs (Fig. 7c). Norway rats preferred eating Serrate oak and Oil tea on naked ground (Fig. 7d). All the four species of rodents preferred eating Serrate oak on naked ground.

There were significant differences in microhabitat selection from natural condition of microhabitat in the enclosure when Edward's long-tailed rats cached seeds of all the three tree species ($p < 0.001$ for all the three tree species). Edward's long-tailed rats preferred caching all the three seed species under grass or shrubs (over 50%) to on naked ground (Fig. 7e).

5. Discussion

According to competition theory, sympatric animals must partition resource exploitation, otherwise, they could not co-exist (Begon et al., 1986). In our study, the four rodent species differed in seed consumption preference. Edward's long-tailed rats preferred consuming seeds of trees, but Norway rats did not like seeds of trees (Fig. 2). The reason why they differed in seed consumption preference might be that they had been evolved to live in different habitats. Edward's long-tailed rats and Chestnut rats usually inhabit forests, while Himalayan rats usually inhabit farmland, and Norway rats usually inhabit houses. Himalayan rats and Norway rats enter the forest only occasionally and crop seeds are their favorite food items.

Garb et al. (2000) hypothesized that larger species of rodents ate larger seeds. Yom-Tov (1991) suggested
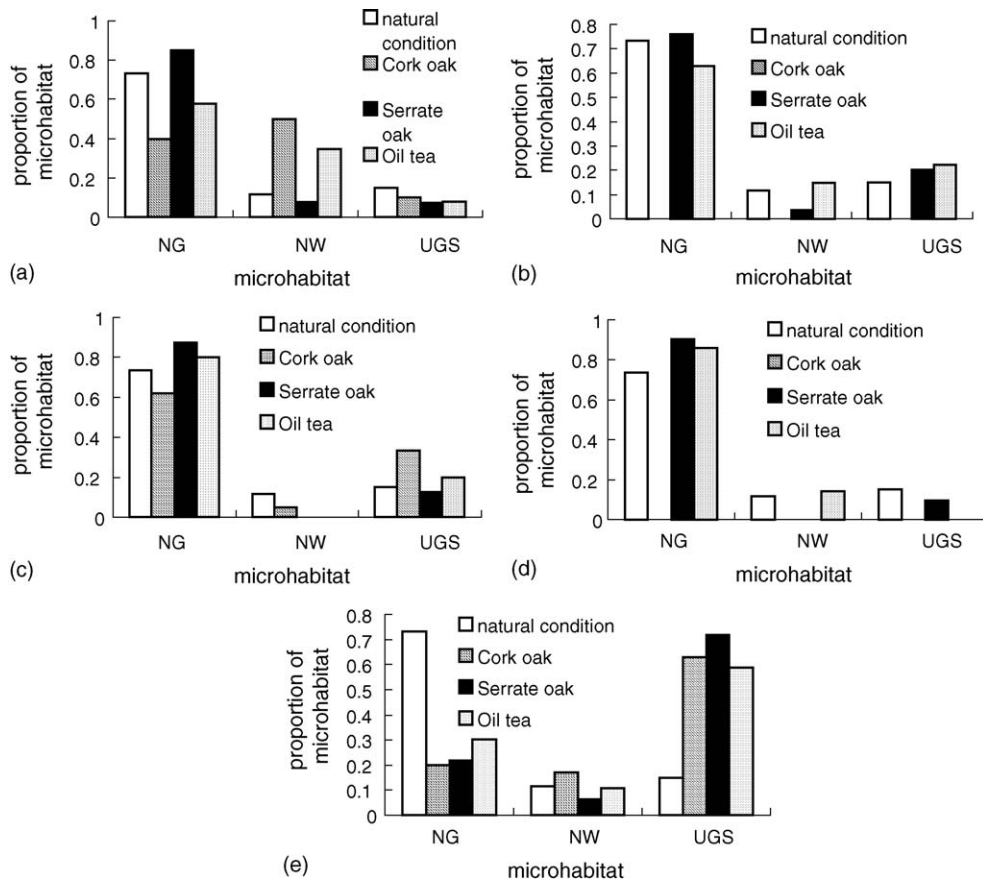
Fig. 7. Microhabitat selection of four rodent species when they ate (a–d) or cached (e) seeds of three tree species. (a) Microhabitat selection of Edward's long-tailed rats when they ate seeds of three tree species. (b) Microhabitat selection of Chestnut rats when they ate seeds of three tree species. (c) Microhabitat selection of Himalayan rats when they ate seeds of three tree species. (d) Microhabitat selection of Norway rats when they ate seeds of three tree species. (e) Microhabitat selection of Edward's long-tailed rats when they cached seeds of three tree species. NG: naked ground. NW: near the wall of the enclosure. UGS: under grass or shrubs.

that rodents might partition seeds according to seed size after measuring the lengths of cheek tooth rows in co-occurring species. But Price (1983) and Price and Brown (1983) suggested that co-occurring species that differed in body size collected similarly sized seeds. In our study, only the larger Edward's long-tailed rats and Himalayan rats selected the largest seed of Cork Oak as food items. However, all the four rodent species selected the smaller seeds of Serrate oak and Oil tea. Our study showed that smaller rodents tended to select smaller seeds, but larger rodents selected both smaller and larger seeds.

Previous research works on seed-hoarding by rodents had always considered the hoarders were a guild (several rodent species) (e.g., Vander Wall, 1998; Zhang and Wang, 2001a; Li and Zhang, 2003; Taraborelli et al., 2003). Jenkins and Breck (1998) and Price et al. (2000) reported that all rodents (six or eight species) in their experiment conducted in arena cached (both scatter-hoarded and larder-hoarded) food. But in our study, the four rodent species differed in caching seeds of three tree species; only Edward's long-tailed rats scatter-hoarded seeds of all the three tree species, while the other three rodent species did neither scatter-hoard nor larder-hoard any seed. Rodents are often faced with food scarcity in field conditions (Jenkins and Breck, 1998; Price et al., 2000). It was believed that rodents caching food items for later use in period

of food scarcity (Andersson and Krebs, 1978; Tamura et al., 1999; Vander Wall, 2000). There are two types of food-hoarding: scatter-hoarding and larder-hoarding. In this study, no larder-hoarding of all four rodent species was observed. Previous study in small enclosures (2 m × 2 m) by Xiao et al. (2003) suggested Edward's long-tailed rats showed both scatter-hoarding and larder-hoarding behavior on *L. harlandii*. Scatter-hoarding was thought to be effective in reducing food pilfering by the other rodents (Vander Wall, 1990). Thus, Edward's long-tailed rats might have advantage of occupying food resources over the other rodent species. In fact, Edward's long-tailed rat was the most dominant rodent species in the subtropical forest, which might benefit from its scatter-hoarding behavior in occupying food resources over the other rodent species.

The contributions to trees of the four rodent species were different. It depended on quantities of seeds they consumed, cached and the population abundance of each rodent species. Consumption of seed (predation pressure) by rodents has a direct negative impact on trees, while scatter-hoarding of seeds by rodents has a positive impact because it increases the probability of seed establishing seedling (Schupp, 1993; Willson and Traveset, 2000). Field test confirmed that 3.5% tin-tagged seeds ($n = 400$) of Cork oak in field became young seedlings from the scatter-hoarded caches by rodents (Xiao, personal communication). Thus, only Edward's rat contributed positively to seed regeneration of the three tree species, while the other three rodent species were only purely seed-eaters, and had no benefits to seed regeneration of the three tree species.

Edward's long-tailed rats had important effect on the three plant species. Though they largely consumed the three seed species, they scatter-hoarded all three seeds, especially Cork oak and Oil tea. The cache sizes of the three seed species were all small. A small cache size can be of benefit to plant (Hollander and Vander Wall, 2004), because a cache containing a large number of seeds may be more likely to be detected by foragers (Vander Wall, 1993). Also, seeds and seedlings often suffer higher mortality when there are a large number clumped together (Howe, 1989), often only one or none of the seedling survives. This is most likely because of competition for resources among seedlings (Howe, 1989; McMurray et al., 1997).

Most seeds of the three tree species were cached under grass or shrubs. Some recent studies have indicated that rodents tend to hoard seeds under or nearby shrubs or at the edge of shrubs (Li and Zhang, 2003). Different seedlings under cover always differ in survival. Research on Singleleaf pinon pine (*Pinus monophylla*) (Chambers, 2001; Hollander and Vander Wall, 2004) suggested that Singleleaf pinon pine survived better under shrub. But research on Liaodong oak (*Quercus liaotungensis*) (Zhang, 2001) and Wild apricot (*P. armeniaca*) (Zhang and Wang, 2001b) suggested that dense vegetation cover reduce seedling recruitment because competition for light and water, but medium shade may be important for seedling establishment. Seedling of Cork oak survive better under medium covert (unpublished data). Therefore, Edward's long-tailed rats caching the three seed species under grass or shrubs might bring benefits to the three species of plants.

Many field researches showed that the distance seed was transported by rodents was normally from 5 to 25 m (e.g., Forget, 1991; Lu and Zhang, 2004b). A 10 m × 10 m enclosure seemed yet small to understand transport distance, but we thought transport distance in such an enclosure can explain something in part. According to models of optimal cache spacing (Stapanian and Smith, 1978; Clarkson et al., 1986), seed-hoarding birds and rodents tend to scatter-hoard higher-value food far from the seed source to protect it from competitor. Results of transport distances of the three species of seeds being cached by Edward's long-tailed rats showed that Cork oak and Oil tea were transported much further than Serrate oak. Cork oak is the largest seed among the three species of seeds, Oil tea has the highest caloric value per unit weight (Table 1). As these seeds were cached farther from the release site (seed source), their probabilities of being pilfered by other rodents reduced. Our results tend to support the hypothesis that large seed were dispersed farther than small seed (Stapanian and Smith, 1978; Clarkson et al., 1986).

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References

Alm, U., Birgersson, B., Leimar, O., 2002. The effect of food quality and relative abundance on food choice in fallow deer. Anim. Behav. 64, 439–445.

Andersson, M., Krebs, J., 1978. On the evolution of hoarding behaviour. Anim. Behav. 26, 707–711.

Arjo, W.M., Pletscher, D.H., Ream, R.R., 2002. Dietary overlap between wolves and coyotes in northwestern Montana. J. Mammal. 83, 754–766.

Begon, M., Harper, J.H., Townsend, C.R., 1986. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publicions, Oxford.

Chambers, J.C., 2001. *Pinus monophylla* establishment in an expanding *Pinus-juniperus* woodland: environmental conditions, facilitation, and interacting factors. J. Veg. Sci. 12, 27–40.

Chen, C., 2000. The Dujiangyan Region, pivot sector of assemblage, differentiation and maintenance of bio-diversity in northern part of Hengduan Mountain. Acta Ecol. Sin. 20, 28–34 (in Chinese, with English abstract).

Clarkson, K., Eden, S.F., Sutherland, W.J., 1986. Density-dependence and magpie food hoarding. J. Anim. Ecol. 55, 111–121.

Dixon, M.D., Johnson, W.C., 1997. Effects of caching on acorn tannin levels and Blue Jay dietary performance. The Condor. 99, 756–764.

Forget, P.M., 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. Trop. Ecol. 32, 155–167.

Forget, P.M., Milleron, T., Feer, F., 1998. Patterns in post-dispersal seed removal by neo-tropical rodents and seed fate in relation to seed size. In: Newbery, D.M., Prins, H.H.T., Brown, N.D. (Eds.), Dynamics of Tropical Communities. Blackwell Science, Oxford, pp. 25–49.

Garb, J., Kotler, B.P., Brown, J.S., 2000. Foraging and community consequences of seed size for coexisting Negav Desert granivores. Oikos 88, 291–300.

Hadj-Chikh, L.Z., Steele, M.A., Smallwood, P.D., 1996. Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. Anim. Behav. 52, 941–948.

Hollander, J.L., Vander Wall, S.B., 2004. Effectiveness of six species of rodents as dispersers of Singleleaf pinon pine (*Pinus monophylla*). Oecologia 138, 57–65.

Howe, H.F., 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79, 417–426.

Hurly, T.A., Lourie, S.A., 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. J. Mammal. 78, 529–537.

Hutchins, H.E., Hutchins, S.A., Liu, B.W., 1996. The role of birds and mammals in Korean pine (*Pinus koraiensis*) regeneration dynamics. Oecologia 107, 120–130.

Ivan, J.S., Swihart, R., 2000. Selection of mast by granivorous rodents of the central hardwood forest region. J. Mammal. 81, 549–562.

Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den, O.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 and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Wallingford, pp. 209–225.

Jenkins, S.H., Breck, S.W., 1998. Differences in food hoarding among six species of heteromyid rodents. J. Mammal. 79, 1221–1233.

Jenkins, S.H., Peters, R.A., 1992. Spatial patterns of food storage by Merriam's kangaroo rats. Behav. Ecol. 3, 60–65.

Jenkins, S.H., Rothstein, A., Green, W.C., 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. Ecology 76, 2470–2481.

Kitchen, A.M., Gese, E.M., Schauster, E.R., 1999. Resource partitioning between coyotes and swift foxes: space, time and diet. Can. J. Zool. 77, 1645–1656.

Kollmann, J., Schill, H.P., 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio 125, 193–205.

Kronfeld-Schor, N., Dayan, T., 1999. The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. Oecologia 121 (1), 123–128.

Laska, M., Baltazar, J.M.L., Luna, E.R., 2003. Food preferences and nutrient composition in captive pacas, *Agouti paca* (Rodentia, Dasyproctidae). Mammal. Biol. 68, 31–41.

Lewis, C.E., Clark, T.W., Derting, T.L., 2001. Food selection by the white-footed mouse (*Peromyscus leucopus*) on the basis of energy and protein contents. Can. J. Zool. 79, 562–568.

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.

Lu, J.Q., Zhang, Z.B., 2004a. Effects of habitat and season on removal and hoarding of seeds of wild apricot (*Prunus armeniaca*) by small rodents. Acta Oecol. 26 (3), 247–254.

Lu, J.Q., Zhang, Z.B., 2004b. Seed-hoarding behavior of Wild apricot and Liaodong oak by small rodents. Acta Theriol. Sin. 24, 132–138 (in Chinese, with English abstract).

McMurray, M.H., Jenkins, S.H., Longland, W.S., 1997. Effects of seed density on germination and establishment of a native and an introduced grass species dispersed by granivorous rodent. Am. Midl. Nat. 138, 322–330.

Post, D., Reichman, O.J., 1991. Effect of food perishability, distance, and competitors on caching behavior by eastern woodrats. J. Mammal. 72, 513–517.

Price, M.V., 1983. Ecological consequences of body size: a model for patch choice in desert rodents. Oecologia 59, 384–392.

Price, M.V., Brown, J.H., 1983. Patterns of morphology and resource use in North American desert rodent communities. Great Basin Nat. Mem. 7, 117–134.

Price, M.V., Waser, M.M., McDonald, S., 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. J. Mammal. 81, 97–106.

Sako, N., Okamoto, K., Mori, T., Yamamoto, T., 2002. The hardness of food plays an important role in food selection behavior in rats. Behav. Brain Res. 133, 377–382.

Schoener, T.W., 1986. Resource partitioning. In: Kikkawa, J., Anderson, D.J. (Eds.), Community Ecology: Pattern and Process. Blackwell Scientific, Melbourne, pp. 91–126.

Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108, 15–29.

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

Silva, M.G., Tabarelli, M., 2001. Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. Acta Oecol. 22, 259–268.

Stapanian, M.A., Smith, C.C., 1978. A model for seed scatter-hoarding: co-evolution of fox squirrels and black walnuts. Ecology 59, 884–898.

Tamura, N., Hashimoto, Y., Hayashi, F., 1999. Optimal distances for squirrels to transport and hoard walnuts. Anim. Behav. 58, 635–642.

Taraborelli, P.A., Dacar, M., Giannoni, S.M., 2003. Effect of plant cover on seed removal by rodents in the Monte Desert (Mendoza, Argentina). Aust. Ecol. 28, 651–657.

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

Vander Wall, S.B., 1993. A model of caching depth: implications for scatter hoarders and plant dispersal. Am. Nat. 141, 217–232.

Vander Wall, S.B., 1998. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. Ecology 79, 233–241.

Vander Wall, S.B., 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chip-munks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behav. Ecol. 11 (5), 544–549.

Vander Wall, S.B., 2001. The evolutionary ecology of nut dispersal. Bot. Rev. 67, 74–117.

Vander Wall, S.B., Jenkins, S.H., 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behav. Ecol. 14, 656–667.

Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. Trends Ecol. Evol. 17, 379–385.

Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. second ed. CAB International, Wallingford, pp. 85–110.

Xiao, Z.S., Zhang, Z.B., 2004. Small mammals consuming tree seeds in Dujiangyan forest. Acta Theriol. Sin. 24, 121–124 (in Chinese, with English abstract).

Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2003. Observations on tree seed selection and caching by Edwar's long-tailed rat (*Leopoldamys edwardsi*). Acta Theriol. Sin. 23, 208–213 (in Chinese, with English abstract).

Xiao, Z.S., Zhang, Z.B., Wang, Y.S., 2004a. 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., 2004b. Impacts of scatter-hoarding rodents on restoration of oil tea *Camellia oleifera* in a fragmented forest. Forest Ecol. Manage. 196, 405–412.

Xiao, Z.S., Wang, Y.S., Zhang, Z.B., Ma, Y., 2002. Preliminary studies on the relationships between communities of small mammals and habitat types in Dujiangyan Region, Sichuan. Biodiver. Sci. 10, 163–169 (in Chinese, with English abstract).

Yom-Tov, Y., 1991. Character displacement in the psammophile Gerbillidae of Israel. Oikos 66, 237–246.

Zhang, Z.B., 2001. Effect of burial and environmental factors on seedling recruitment of *Quercus liaotungensis* Koidz. Acta Ecol. Sin. 21, 374–384.

Zhang, Z.B., Wang, F.S., 2001a. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). Acta Ecol. Sin. 21, 839–845.

Zhang, Z.B., Wang, F.S., 2001b. Effect of rodent predation on seedling survival and recruitment of wild apricot. Acta Ecol. Sin. 21, 1761–1768 (in Chinese, with English abstract).

Zhang, Z.B., Xiao, Z.S., Li, H.J., 2005. Impact of small rodents on tree seeds in temperate and subtropical forests, China. In: Forget, P.-M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), Seed Fate, Predation, Dispersal and Seedling Establishment. CABI Publishing, Massachusetts, pp. 269–282.