Original article

Differences in hoarding behaviors among six sympatric rodent species on seeds of oil tea (*Camellia oleifera*) in Southwest China

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ABSTRACT

Seed hoarding is an important behavioral adaptation to food shortages for many rodent species. Sympatric rodents may affect the natural regeneration of large-seeded trees differently as seed dispersers or seed predators. Using seeds of oil tea (*Camellia oleifera*), we investigated differences in hoarding behaviors among six sympatric rodent species in semi-natural enclosures in a subtropical forest in southwest of China. We found that all these six species ate seeds of *C. oleifera*, but only Edward's long-tailed rats (*Leopoldamys edwardsi*) were predominantly scatter hoarders; chestnut rats (*Niviventer fulvescens*) and white-bellied rats (*Niviventer confucianus*) scatter hoarded and larder hoarded few seeds, but were seed predators; South China field mice (*Apodemus draco*) exhibited little larder-hoarding behavior; and Chevrier's field mice (*A. chevrieri*) as well as Himalayan rats (*Rattus nitidusa*) did not hoard seeds at all. The rodents that engaged in scatter hoarding often formed single-seed caches and tended to cache seeds under grass or shrubs. Our findings indicate that sympatric rodents consuming seeds of the same species of plant can have different hoarding strategies, affecting seed dispersal and plant regeneration differently. We conclude by discussing the role of these species in hoarding seeds of *C. oleifera* and highlight the essential role of Edward's long-tailed rats as predominantly potential dispersers of this plant species.

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1. Introduction

Food hoarding is an important behavioral adaptation to food shortages for many rodent species (Vander Wall, 1990). Seeds are commonly scatter or larder hoarded by rodents. In larder hoarding, seeds are stored in large quantities in a single or a few sites while in scatter hoarding, one or few seeds are stored at many sites in a relatively large area (Smith and Reichman, 1984; Vander Wall, 1990; Dally et al., 2006). Differences in seed hoarding behaviors may be important in promoting species coexistence (Jenkins and Breck, 1998; Price et al., 2000; Leaver and Daly, 2001). Most previous studies of hoarding behavior focus on single species (e.g. Jenkins and Peters, 1992; Clarke and Kramer, 1994a,b; Jenkins et al., 1995; Vander Wall et al., 2001; Leaver, 2004), but studies at the community level with multiple sympatric species are relatively rare (but see Jenkins and Breck, 1998; Price et al., 2000; Hollander and Vander Wall, 2004).

Seed dispersal among rodent guilds is a complex process in determining dispersal fitness and seedling establishment of trees (Forget et al., 2005; Gomez et al., 2008). Differential hoarding behavior can often result in different outcomes in terms of seed dispersal and seedling success. Larder hoarding is thought to be less beneficial to plants than scatter hoarding (Vander Wall, 1990). Furthermore, factors such as cache size and cache microhabitat, are also important for seed survival (Hollander and Vander Wall, 2004). How rodent species differ in their hoarding behaviors which in turn influences the effective dispersal of seeds and thereby forest regeneration is still unclear. Seed hoarders often consume many of the cached seeds and thus impose a negative effect on seedling recruitment (Hulme, 2002; Mendoza and Dirzo, 2007). However, scatter hoarding animals can provide effective seed dispersal resulting in successful seedling establishment by burying seeds in shallow soil over a large area (Vander Wall, 2001).

Seed dispersal and hoarding by rodents have been investigated under field conditions by using the seed tagging method in recent years (e.g. Xiao et al., 2006a, 2008; Xiao and Zhang, 2006; Moore et al., 2007; Gomez et al., 2008; Zhang et al., 2008; Yi and Zhang, 2008). However, it is very difficult or even impossible to distinguish the differential effect of sympatric rodent species by using this method in the field. To understand the differential impact of sympatric seed-eating rodents on seed fates, we conducted

observations in semi-natural enclosures on six sympatric rodent species: Edward's long-tailed rats (*Leopoldamys edwardsi*), chestnut rats (*Niviventer fulvescens*), white-bellied rats (*Niviventer confucianus*), Chevrier's field mice (*Apodemus chevrieri*), South China field mice (*Apodemus draco*) and Himalayan rats (*Rattus nitidusa*). *Camellia oleifera* (Theaceae) is an important shrub species in China and while once widely distributed, has suffered from deforestation and urban expansion. Its value is both economic and environmental since the majority of *C. oleifera* is now confined to stands of primary forest that require management and ongoing monitoring. Understanding the effect of seed hoarding behavior on seeds of *C. oleifera* allows us to develop both our understanding of sympatric seed-hoarding behavior and the effect of seed-hoarding rodents on the dispersal of this plant species.

2. Materials and methods

2.1. Study site and study species

This study was conducted in an experimental forest in Dujiangyan forest, Sichuan, China (700 to 1000 m a.s.l.; 31° 4′ N, 103° 43′ E) from September to December in 2005 and 2006. The area is characterized by subtropical evergreen broadleaf forest. Historically, *C. oleifera* was widely distributed throughout the region but the number of trees has declined due to deforestation. Currently, the majority of *C. oleifera* is found in primary forest between 80 and 90 years old, with few individuals occurring in secondary stands (<50 years) or shrub lands (~ 10 years) (Xiao et al., 2004). *C. oleifera* flowers from late September to November and fruit ripening takes place in September of the following year. After ripening, *C. oleifera* fruit naturally dehisces and falls under or near parent trees. Each fruit contains between one and eight seeds (mean seed weight $\pm$ SE $= 0.87$ g ± 0.07 g, $n = 60$). *C. oleifera* seeds are strictly rodent-dispersed, and natural regeneration depends largely on seed-hoarding rodents (Xiao et al., 2004; Wang et al., 2004; Cheng et al., 2005a).

To trap animals, we used large wired cage traps (30 cm × 25 cm × 20 cm) baited with peanuts (for food) and cabbage (for water) and provisioned with local dry leaves as nest material. The traps and nesting material protected rodents from cold weather and predators. Traps were deployed between 1900 h to 1930 h and checked after 12 h. All captured animals were then transferred to our laboratory for housing except for pregnant or lactating females or juveniles which were released immediately. Prior to experimentation, all animals were housed individually in a large mouse cage (50 cm × 30 cm × 25 cm) containing nesting material. The housing room was maintained at 10–15 °C with a natural light/dark cycle (12L:12D); food and water were provided *ad libitum*. All procedures complied with guidelines for animal use and care as stipulated by the Institute of Zoology, Chinese Academy of Sciences.

In this study, we used 25 adult Edward's long-tailed rats (10 ♂, 15 ♀), 14 adult chestnut rats (9 ♂, 5 ♀), 11 adult white-bellied rats (4 ♂, 7 ♀), 5 adult Chevrier's field mice (4 ♂, 1 ♀), 7 adult South China field mice (6 ♂, 1 ♀) and 9 adult Himalayan rats (5 ♂, 4 ♀). At the close of the experimental period (two to three months duration) all animals were released at the site of capture.

2.2. Observations and enclosure design

Observations were conducted in four 10 × 10 m semi-natural enclosures. The enclosures were built with bricks, and the walls of the enclosures extended 1.5 m above and 0.5 m below ground. The walls were smooth and the tops of enclosure were covered with a piece of large plastic cloth supported by a steel frame. These measures effectively prevented subjects from escaping and predators from entering the enclosures. A layer of periodically watered sand, about 5–8 cm thick, was spread in the enclosure to simulate the soft soil of the forest. The habitat in the enclosures was similar to and typical of the study area, consisting of a variety of shrubs and herbaceous plants (but without trees). The plant distributions in all four enclosures were similar and the area of plants in each enclosure was about 15 m². A nest box (18 cm × 18 cm × 40 cm) was buried underground at the corner of each enclosure. A single sloping PVC pipe (25 cm diameter, 40 cm long) connected the underground burrow with the ground surface, permitting rodents to enter or leave the nest. A total of 95% rodents used the box as their burrow during the experiment.

To habituate animals to the testing environment, each animal was introduced into the enclosure one night prior to observation. Observations of seed hoarding behavior were conducted over two consecutive nights for each individual. At 1730 h the first day we presented one individual with 50 *C. oleifera* seeds with small coded plastic tags; tagging has been shown to have a negligible effect on seed removal and hoarding (Xiao et al., 2006b). At 0730 h the next day we scoured the enclosure and recorded the fate of each seed, including cache size and microhabitat in which the rodents stored their caches, either in the open or under grass and shrubs. Then we removed all seeds and repeated the procedure for a second night. Seed fates were defined as follows: harvested (removed from the seed station and included eating and hoarding); eaten (gnawed open with the entire or majority of the kernel consumed); scatter hoarded (intact seeds buried in soil or grass); and larder hoarded (intact seeds which were stored in the burrow). Seeds that were removed from the station but left intact on the ground were not included in the analysis.

2.3. Statistical analyses

We combined seed fate data from both observation nights to obtain a record of hoarding behavior for each animal. All statistical analyses were performed using R version 2.8.0 (Crawley, 2007). We used Generalized Linear Models (GLM) to explore differences in four seed fates among all six species. Count data were log ($x + 1$) transformed and response variables were fitted to a Poisson distribution. One-way ANOVAs were used to test for differences in the microhabitat of cached seeds and Kruskal–Wallis tests were used to test for differences in cache size (proportion data were arcsine-square-root transformed). Independent-samples t tests were used to examine the differences in hoarding behaviors between males and females (count data were log ($x + 1$) transformed for normal distribution). All statistical tests are two-tailed, and the alpha level was set at 0.05.

3. Results

3.1. Rodent species and dominance

We captured a total of 184 target animals. Edward's long-tailed rats were the most dominant species and comprised nearly half of all captures (46.7%). Chestnut rats were the second dominant species (21.7%) while the other four species, white-bellied rats (9.8%), Chevrier's field mice (3.3%), South China field mice (8.7%) and Himalayan rats (7.1%) were less dominant (see Fig. 1).

3.2. Difference in hoarding behaviors

All six rodent species were found to harvest and eat *C. oleifera* seeds, and we found significant differences in seed harvesting behavior (GLM, $Z_{5,71} = 2.48$, $P = 0.01$), but not consumption (GLM, $Z_{5,71} = 0.97$, $P > 0.05$). The six rodent species exhibited significant and different scatter-hoarding behavior (GLM, $Z_{5,71} = 5.71$, $P < 0.01$);
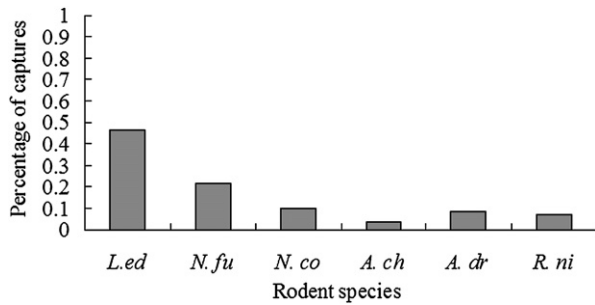
Fig. 1. Percentage (%) of six sympatric rodent species in total captured animals (*L. ed*, Edward's long-tailed rats; *N. fu*, chestnut rats; *N.co*, white-bellied rats; *A. ch*, Chevrier's field mice; *A. dr*, South China field mice and *R. ni*, Himalayan rats) in the Dujiangyan region, Sichuan, China.
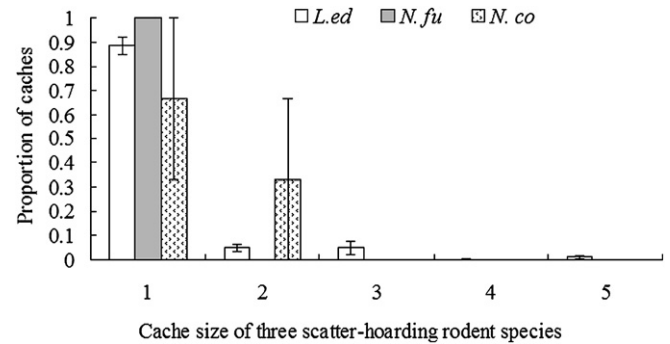

Fig. 2. Cache size (mean ± S.E.) of the three scatter-hoarding rodent species (Edward's long-tailed rats, $N = 23$; chestnut rats, $N = 5$; white-bellied rats, $N = 2$) in the experimental enclosures in the Dujiangyan region, Sichuan, China.

only Edward's long-tailed rats, chestnut rats and white-bellied rats scatter hoarded seeds. Few animals of the six species larder hoarded seeds and there was no difference in this behavior among species (GLM, $Z_{5,71} = 0.806$, $P = 0.42$) (see Table 1). Furthermore, we found differences in hoarding behavior between males and females for Edward's long-tailed rats only; males scatter hoarded more seeds than females (independent-samples, $t_{48} = 2.21$, $P = 0.03$).

3.3. Difference in cache size and microhabitat

Among the species which scatter-hoarded seeds the majority of caches contained only a single seed (Fig. 2) and were usually placed under grasses or shrubs (Fig. 3). We found significant differences neither in cache size (the number of seeds per cache) (Kruskal–Wallis, $H_{2,23} = 1.34$, $P > 0.05$) nor in seed microhabitat (the location of the cache) (ANOVA, $F_{2,27} = 0.73$, $P > 0.05$) among species.

4. Discussion

4.1. Difference in hoarding behaviors

When seed-eating rodents encounter food they often have two decisions: eat them *in situ* or transport them into other places (Lima and Valone, 1986; Shimada, 2001). Our results showed that all the six sympatric rodent species harvested and consumed *C. oleifera* seeds from the feeder, but they hoarded them very differently. Edward's long-tailed rats were predominantly scatter hoarders although they also larder hoarded a small number of seeds. Chestnut rats and white-bellied rats scatter hoarded and larder hoarded seeds; however, only a few individuals exhibited hoarding behavior and the quantities which they hoarded were very small. South China field mice showed very little larder hoarding behavior and together with Chevrier's field mice and Himalayan rats (that did

not hoard seeds at all) should be classed as seed predators. Our studies therefore suggest that Edward's long-tailed rats play an essential role in natural seeding regeneration of *C. oleifera*.

Our studies demonstrate that sympatric rodent species differ greatly in hoarding behaviors of tree seeds. This observation is well in agreement with several other studies. For example, Price et al. (2000) investigated the differences of hoarding behavior among eight species of kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus* and *Chaetodipus*) in an indoor arena. They found that kangaroo rats scatter hoarded more seeds than sympatric pocket mice. Lu and Zhang (2004) found several sympatric rodents consumed seeds of wild apricot (*Prunus armeniaca*), but only the large field mouse (*Apodemus peinsulae*) scatter hoarded these seeds.

Food hoarding is very essential for rodents to overcome periods of food shortage or to ensure food supply during breeding seasons (Vander Wall, 1990). Given the prevalence of seed hoarding behavior in rodents, it is surprising that we detected scant hoarding behavior of *C. oleifera* seeds by some species. On the one hand, this result may be affected due to small sample size for some species. On the other hand, in our previous studies of the same site, we have found that Chevrier's field mice and South China field mice scatter-hoarded oak seeds, such as *Quercus variabilis* and *Q. serrata* (Chang et al., 2006, 2009). Differentiation in hoarding preference among sympatric rodent species may facilitate their coexistence (Jenkins and Breck, 1998). In field conditions, sympatric species may interact with each other and this may have an important influence on their hoarding behaviors (Dally et al., 2006). The presence of competitors may increase caching efforts as rodents may want to garner as many seeds as possible (Mappes, 1998; Cheng et al., 2005b). Lack of competitors may partially explain the scant hoarding behaviors of some species in the study.
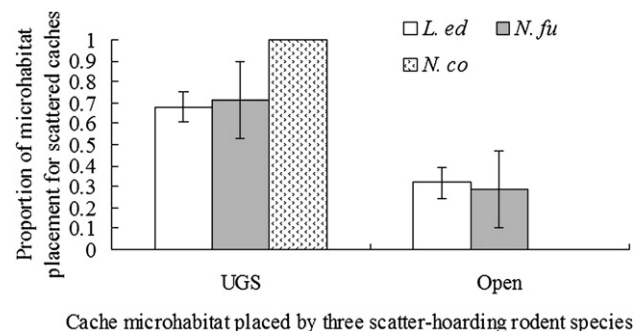
Table 1
Seed fates of *Camellia oleifera* handled by the six sympatric rodent species in the Dujiangyan region, Sichuan, China (values are mean number of seeds ± SE).

Rodent species	Seed fate (number of seeds, $N = 50$)[a]			
	Harvested[b]	Eaten	Scatter hoarded	Larder hoarded
Edward's long-tailed rats ($N = 25$)	19.2 ± 2.1	9.1 ± 0.8	9.0 ± 1.8	0.6 ± 0.4
Chestnut rats ($N = 14$)	11.0 ± 0.9	9.6 ± 0.8	0.3 ± 0.1	0.3 ± 0.2
White-bellied rats ($N = 11$)	12.1 ± 1.9	11.2 ± 1.8	0.2 ± 0.2	0.4 ± 0.3
Chevrier's field mice ($N = 5$)	4.8 ± 2.2	4.8 ± 2.2	0	0
South China field mice ($N = 7$)	11.4 ± 2.3	10.8 ± 2.2	0	0.2 ± 0.2
Himalayan rats ($N = 9$)	6.3 ± 2.4	6.3 ± 2.41	0	0

[a] Average for both nights.
[b] Seeds that were removed from the station but left intact on the ground were not included in the analysis.

Fig. 3. Difference (mean ± S.E.) in microhabitat of scattered caches by the three scatter-hoarding rodent species (Edward's long-tailed rats, $N = 23$; chestnut rats, $N = 5$; white-bellied rats, $N = 2$) in the experimental enclosures in the Dujiangyan region, Sichuan, China (UGS, under grass or shrubs; Open, naked ground).

There were significant hoarding differences between males and females of Edward's long-tailed rats, the only species that scatter hoarded *C. oleifera* seeds in this study. Also, male Edward's long-tailed rats scatter hoarded a higher proportion of seeds than females. This difference may be explained by differences in memory and physiology between male and female rodents. For example, Barkley and Jacobs (2007) found that the capacity of retrieving caches by female Merriam's kangaroo rats (*Dipodomys merriami*) was significantly impaired by the absence of local landmarks compared to that of males. Female spatial performance was found to decrease during the breeding season as compared with that during the non-breeding season, whereas the reverse pattern was observed in males in deer mice (*Peromyscus maniculatus*) (Galea et al., 1996). Males of Pinyon jays (*Gymnorhinus cyanocephalus*) are able to accurately recover caches made by their mates, whereas females do not show this ability (Dunlap et al., 2006). However, some studies have shown no difference between males and females in the anatomy of the hippocampus, or in food storing, or memory for food caches, e.g. in black-capped chickadees (*Parus atricapillus*) (Petersen and Sherry, 1996). Thus it is necessary to investigate the underlying mechanism for sexual differences in hoarding behavior of rodents in future studies.

4.2. Difference in cache size and microhabitat

The proportion of harvested seeds that is scatter hoarded is an important index influencing final seedling establishment because seeds that are larder-hoarded in burrows do not contribute to natural regeneration (Hollander and Vander Wall, 2004). In this study, we found that between 0% and 47% of seeds that were harvested were subsequently scatter hoarded. This pattern was strongest in Edward's long-tailed rat which scatter hoarded nearly half of the seeds it harvested. Therefore, it is clear that Edward's long-tailed rats are potential dispersers of *C. oleifera* seeds in our study site.

Single-seeded caches may have a better effect on seedling establishment than many-seeded caches. (Hollander and Vander Wall, 2004). Seedlings emerged from clumped seeds often suffer high mortality because of intensive inter-seedling competition for limited resources and space (Howe, 1989). Besides, larger caches are more likely pilfered by foragers (Vander Wall, 1993). In this study, 86% animals placed one seed in each cache site, and this strategy is favorable to seedling establishment in natural conditions (Xiao et al., 2004). The microhabitat selected by rodent for storing seeds could be very important for successful seedling establishment. We found Edward's long-tailed rats, chestnut rats and white-bellied rats placed the majority of their caches under grass or shrubs which are suitable for seedling establishment. In single-leaf pinon pine (*Pinus monophylla*), seeds were found to survive better under shrub habitats which have suitable soil temperature, moisture and nutrient content (Chambers, 2001; Hollander and Vander Wall, 2004). Our previous studies also found that seeds, such as Liaodong oak (*Quercus liaotungensis*) and wild apricot (*Prunus armeniaca*), which had been buried under shrubs or grass, had higher survival time and seedling establishment than those which had been buried under naked ground (Li and Zhang, 2003; Lu and Zhang, 2004; Zhang et al., 2008).

4.3. Conclusion

In summary, we found sympatric rodent species differ greatly in hoarding behaviors of *C. oleifera* seeds; Edward's long-tailed rats were the predominantly scatter hoarders of *C. oleifera* seeds. Most scatter-hoarded caches contained a single seed, and they were stored mainly under grass or shrubs, which may be beneficial to seedling establishment under natural condition. Edward's long-tailed rats play an essential role in maintaining the natural seedling regeneration of *C. oleifera* in the study region.

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