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ORIGINAL ARTICLE

Does scatter-hoarding of seeds benefit cache owners or pilferers?

Haifeng GU,[1,2] Qingjian ZHAO[2] and Zhibin ZHANG[1]

[1]State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, China and [2]University of Chinese Academy of Sciences, Beijing, China

Abstract

The scatter-hoarding behavior of granivorous rodents plays an important role in seed dispersal and seedling regeneration of trees, as well as the evolution of several well-known mutualisms between trees and rodents in forest ecosystems. Because it is difficult to identify seed hoarders and pilferers under field conditions by traditional methods, the full costs incurred and benefits accrued by scatter-hoarding have not been fully evaluated in most systems. By using infrared radiation camera tracking and seed tagging, we investigated the benefits and losses of scatter-hoarded seeds (*Camellia oleifera*) for 3 sympatric rodent species (*Apodemus draco*, *Niviventer confucianus* and *Leopoldamys edwardsi*) in a subtropical forest of Southwest China during 2013 to 2015. We established the relationships between the rodents and the seeds at the individual level. For each rodent species, we calculated the cache recovery rate of cache owners, as well as conspecific and interspecific pilferage rates. We found that all 3 sympatric rodent species had a cache recovery advantage with rates that far exceeded average pilferage rates over a 30-day tracking period. The smallest species (*A. draco*) showed the highest rate of scatter-hoarding and the highest recovery advantage compared with the other 2 larger species (*N. confucianus* and *L. edwardsi*). Our results suggest that scatter-hoarding benefits cache owners in food competition, supporting the pilferage avoidance hypothesis. Therefore, scatter-hoarding behavior should be favored by natural selection, and plays a significant role in species coexistence of rodent community and in the formation of mutualism between seeds and rodents in forest ecosystems.

Key words: Chinese white-bellied rat, Edward's long-tailed rat, oil tea, scatter-hoarding benefits, South China field mouse

INTRODUCTION

Food hoarding is a general strategy used by animals to store food in caches for surviving periods of food scarcity (Vander Wall 1990). Most commonly, seeds are cached because they have high nutritional value (Smith & Reichman 1984). Meanwhile, seeds are crucial to plant regeneration for many plant species (Howe & Smallwood 1982; Chambers & Macmahon 1994). Af-

Correspondence: Zhibin Zhang, State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.
Email: zhangzb@ioz.ac.cn

ter leaving the parent plant, seeds have to be dispersed away from maternal sources and ultimately reach microsites suitable for establishment (Chambers & Macmahon 1994). Granivorous rodents are especially important in dispersing seeds because of their preference for hoarding seeds and their coincidental selection of such microsites (Stapanian & Smith 1978; Howe & Smallwood 1982; Vander Wall 1990; Jenkins *et al.* 1995; Zhang & Wang 2000; Vander Wall *et al.* 2001; Xiao *et al.* 2002; Zhang *et al.* 2008; Pan *et al.* 2016). Although a majority of seeds are finally consumed by rodents, a small proportion survives from predation by rodents and develops into seedlings because cache owners regularly fail to retrieve the cached seeds (Janzen 1971; Howe & Smallwood 1982; Vander Wall 1990). Consequently, the interaction between plants and rodents is both antagonistic and indirectly mutualistic from the perspective of seed hoarding and consumption, often shifting back and forth under different environmental conditions (Chambers & Macmahon 1994; Zhang *et al.* 2015, 2016b,c).

Not all seed hoarding strategies are beneficial to regeneration of plants. Seed-hoarding strategies of rodents can form a spectrum, ranging from larder-hoarding to scatter-hoarding (Vander Wall 1990). Larder-hoarding involves hoarding a large number of seeds in a single cache, such as in a burrow chamber of rodents (Blair 1937), while in scatter-hoarding, seeds are sequestered in scattered positions, such as one seed at each cache site (Morris 1962; Vander Wall 1990). Scatter-hoarding is expected to favor germination because of the wider dispersion of seeds across suitable microenvironments and a lower recovery rate by seed predators compared to larder-hoarding (Vander Wall 1990, 2001).

It is not fully understood why rodents adopt a scatter-hoarding strategy because establishing, protecting and retrieving numerous scattered caches may require considerable energy costs as well as increase predation risks to the hoarders (Jenkins & Peters 1992; Steele *et al.* 2015). Several hypotheses have been proposed to explain the rationale of scatter-hoarding behavior. Jenkins and his colleagues (Jenkins & Peters 1992; Jenkins *et al.* 1995) proposed a rapid sequestering hypothesis based on laboratory studies on Merriam's kangaroo rats (*Dipodomys merriami* Mearns, 1890). They suggested that rodents scatter-hoarded seeds nearby seed sources to reduce travel costs for transferring seeds and to maximize harvest rates. When seeds availability dropped, the kangaroo rats could re-distribute caches more widely. Stapanian and Smith (1978) proposed the pilferage avoidance hypothesis based on field tests of fox squirrels (*Sciurus niger* Linnaeus, 1758) scatter-hoarding black walnuts (*Juglans nigra*). Their model suggested that some rodents scatter-hoarded seeds because they were not able to defend larders against pilferers. Both the rapid sequestering and pilferage avoidance hypotheses predict that the proportion of cache pilferage should be very low so as to ensure benefits of cache owners. In contrast, Vander Wall and Jenkins (2003) proposed the reciprocal pilferage hypothesis based on a review of several experimental studies on cache pilferage. They found that the proportion of cache pilferage was quite high (over 70%) for many species in which pilferage was studied by using artificial caches. They suggested rodents could endure pilfering and ensure their own benefits if they also pilfered the caches of other rodents. This hypothesis was also supported by a field study conducted by Jansen *et al.* (2012). Unfortunately, to date, most previous studies on pilferage rates have been conducted in small enclosures or with artificial interventions to simulate "pilferage" (using artificial caches) (Vander Wall 2003). As a result, little information is known about the real pilferage rates under field conditions (but see Stapanian & Smith 1978; Steele *et al.* 2011; Jansen *et al.* 2012).

Due to the difficulty of traditional methods in identifying the seed hoarders and pilferers under field conditions, links between individual seeds and scatter-hoarding animals are hard to establish. Thus, the hypotheses above are seldom tested under field conditions based on observations of the relationship between seeds and rodents at individual level (but see Jansen *et al.* 2012). Traditional methods to track seed dispersal, including direct observation (Morris 1962; Stapanian & Smith 1978), metal marking (Sork 1984), thread marking (Forget 1990), fluorescent marking (Longland & Clements 1995; Levey & Sargent 2000), radioactive isotope marking (Lawrence & Rediske 1960; Abbott & Quink 1970; Hollander & Vander Wall 2004) and wire tin/plastic-labelled seed tagging (Zhang & Wang 2000; Xiao *et al.* 2008), are not able to distinguish individual seed dispersers. Recently, a method combining very high frequency (VHF) radio transmitter and infrared radiation (IR) camera tracking was proposed by Jansen *et al.* to identify both the seed dispersers and seed fates, and to calculate the rates of pilferage of seeds (such as *Astrocaryum standleyanum*, weighing approximately 10 g) dispersed by rodent species (such as *Dasyprocta punctata* (Gray, 1842), weighing approximately 2 to 4 kg); the results indicated that the pilferage was very common (Jansen *et al.* 2012). This method allows us to calculate the true pilferage rates under field conditions, but it cannot be readily applied to study seed dispersal and pilferage of small seeds by small rodents due to the relatively large size of the radio transmitters (often >4 g).

In the present study, we tested the pilferage avoidance hypothesis and the reciprocal pilferage hypothesis based on observations of individual relationship between seeds and rodents by adopting a seed tagging and IR camera tracking method that enabled us to identify individual small-sized seeds (approximately 1 g) and rodents (<500 g) under field conditions. By tracking tagged seeds and marked rodents using an IR camera, we were able to identify the individual seed and its dispersers. Thus, this method allowed us to evaluate the benefits of scatter-hoarding of seeds to cache owners and pilferers, and some specific scatter-hoarding strategies the rodent species used (including the hoarding preference and competition efficiency).

MATERIALS AND METHODS

Study site

Our study site was located in the Banruosi (Prajna Temple) Experimental Forest (31°3′N, 103°43′E, elevation 700–1000 m) near Dujiangyan City, Sichuan Province, Southwest China. The mean annual temperature was approximately 10 °C, and the annual precipitation was 1300–1800 mm. The site was a subtropical evergreen broad-leaved forest known for its high biodiversity due to a warm, wet climate and variable topography (Chen 1999). Local common tree species with large-sized seeds include *Acer catalpifolium*, *Camellia oleifera*, *Castanopsis fargesii*, *Cyclobalanopsis glauca*, *Lithocarpus harlandii*, *Phoebe zhennan*, *Pinus massoniana*, *Quercus serrata* and *Quercus variabilis* (Xiao *et al.* 2006). Rodent species consuming or dispersing seeds of these plant species include *Apodemus draco* (Barrett-Hamilton, 1900), *Apodemus chevrieri* (Milne-Edwards, 1868), *Apodemus latronum* Thomas, 1911, *Berylmys bowersi* (Anderson, 1879), *Leopoldamys edwardsi* (Thomas, 1882), *Niviventer confucianus* (Milne-Edwards, 1871), *Niviventer fulvescens* (Gray, 1847), *Micromys minutus* (Pallas, 1771) and *Rattus nitidus* (Hodgson, 1845) (Xiao *et al.* 2002).

We selected a 0.5-ha plot on a hilltop (31°3′47″N, 103°43′26″E) northeast of the Prajna Temple. The plot represented the typical vegetation and environment in the study region well. A preliminary survey conducted in April 2013 indicated that there were 3 rodent species in the plot: South China field mice (*A. draco*, mean weight ≈ 20 g), Chinese white-bellied rats (*N. confucianus*, mean weight ≈ 70 g), and Edward's long-tailed rats (*L. edwardsi*, mean weight ≈ 300 g) (Wilson & Reeder 2005, Fig. 1). We chose seeds of oil tea (*C. oleifera*) to study hoarding behaviors of these sympatric rodent species. *C. oleifera* are small evergreen broad-leaved trees and abundant in the region as well as the entire Southwest China. They produce capsules containing 1–10 seeds that ripen during September to Novem-

Figure 1 Species in the study and the arrangement of a seed station. (a) Mature fruits and seeds of oil tea, *Camellia oleifera*; (b) *Apodemus draco*; (c) *Niviventer confucianus*; (d) *Leopoldamys edwardsi*; (e) A seed station with an IR camera attached to a tree stem, and coded and tagged seeds on the ground.

ber. A single seed weighs 0.84 ± 0.38 g (mean ± SD, *n* = 996) and has a low tannin content but a high fat content (> 50%). Many local rodent species prefer to consume and hoard oil tea seeds (Xiao *et al.* 2002; Xiao & Zhang 2003), leaving empty capsules on the ground to decay.

Animal trapping and marking

All our experiments were conducted from May 2013 to November 2015. The experiment of 2013 was conducted from late March to early May, and from mid-August to mid-October. The experiment of 2014 was conducted in January, and from October to December. The experiment of 2015 was conducted in late January, and from July to November). We divided the plot into 6 × 11 grids with intervals of 10 m, and set a live trap at the center of each grid, forming a matrix of 66 live traps in the plot with 10-m spacing between adjacent traps (Fig. S1). The traps (length × width × height = 30 × 15 × 14 cm) were made of 1-cm^2 steel wire mesh. Each trap was baited with a fresh seed of local Chinese chestnut (*Castanea mollissima*), which was another favored food item of local rodents. All traps were checked and re-set early each morning. Captured rodents were identified, weighed, marked with unique and distinguishable patterns on the back with wine-red human hair dye (Steele *et al.* 2008; Zhao *et al.* 2016) and then released *in situ*. Recaptured individuals, juveniles and pregnant females were released immediately without marking (we only captured 2 pregnant females during the entire 3 year-period). The process continued until there was no new captive in the entire plot for 2 successive days. During later experiments, we re-dyed some animals before their dye marks faded. We conducted animal trapping at the beginning of the experiment period each year. All animal trapping and handling procedures were approved by the Institute of Zoology, Chinese Academy of Sciences (Ethical Inspection License No: IOZ13034). Principles of Laboratory Animal Care (revised by the US National Institutes of Health) were followed during the entire process.

Seeds tagging and tracking

We collected ripe fruits of the oil tea (*C. oleifera*) at least 500 m away from the study site and air-dried seeds naturally after removing the capsules (Fig. 1). All seeds were tagged with 10-cm-long thin steel wires and plastic labels (2.5 × 3.6 cm, with seed codes of date and station number of placement marked on tags) by following the protocols of seed tagging (Xiao *et al.* 2008) with the modification that the plastic labels were cut into 10 different shapes for individual identification of each seed (Zhao *et al.* 2016). IR cameras were used to identify individual seed by tag shapes and individual rodent by dye marks during the period of seed tracking (Fig. 1). Each seed was weighed before placement.

We selected 10 seed stations in the center of the plot spaced at 20-m intervals to place tagged seeds (Fig. S1). At each station, 10 tagged seeds with unique codes reflected in different tag shapes were placed evenly on the soil surface within a 0.5-m^2 quadrat, following the animal-trapping and marking. Each year, a total of 100 seeds were placed at the beginning of the seed tracking. Additional seeds were added continuously when seeds at the seed stations were removed or consumed *in situ* by rodents. A total of 1905 seeds were placed over the 3 years (835 seeds in 2013, 630 in 2014 and 440 in 2015).

At each seed station, we chose a healthy and firm tree nearby and attached a Ltl-5210A IR camera (manufactured by Little Acorn Outdoors, Green Bay, USA) set on video record mode (Video Size: 640 × 480; PIR Sensitivity: High; Video Length: 10 s; Trigger Interval: 0 s) to monitor seed harvest and dispersal by rodents (Fig. 1). By identifying dye marks and tag shapes in footage, the relationship between individual seeds and rodents was established. However, a certain portion of observations (19.9% of the rodent-harvested seeds) were not successful due to camera failure.

Every day from 0800 to 1600 hours after seeds were placed, we searched the area around the seed stations within a radius of 30 m to locate the dispersed seeds. This was based on previous observations that the majority of oil tea seeds were dispersed within 20 m of their sources (Xiao *et al.* 2004). By following our previous studies (Zhang *et al.* 2008; Huang *et al.* 2011), seed fates were defined as intact *in situ* (IIS), eaten *in situ* (EIS), eaten after being removed (EAR), scatter-hoarded (SH) or missing (M). IIS indicates intact seeds that were not removed by rodents from seed stations. EIS indicates seeds that were eaten at seed stations. EAR indicates seeds that were eaten after being removed away from seed stations. SH indicates seeds that were scatter-hoarded by rodents in soil or litter layers. M indicates seeds that were not retrieved by observers; they might either be larder-hoarded in burrows or dispersed far away beyond the searching radius. For each seed, we recorded the dates and distance of seed dispersal; seed fates; and the approximate location, depth, substrate and type of microhabitat of the cache (if the seed was cached). We set an IR camera near each scatter-hoarded seed that we retrieved, and then monitored their fate (re-caching or pilferage) and identified the individuals that harvested the seeds where possible. This method enabled us to identify seed retention by cache owners and interspecific or con-specific seed pilferage by other individuals. The camera tracking procedure was stopped when all seeds were finally consumed or missing, or no further dispersal of cached seeds was observed for 30 successive days (Stapanian & Smith 1978).

By using seed tagging and IR camera tracking, we established the relationships between nearly every individual seed and the individual rodent that harvested (cached or ate) it (80.1% of 1083 rodent-harvested seeds). As shown in Fig. 2, initial harvested seeds (IHS) of a rodent species were composed of seeds removed from seed stations (R) and seeds eaten *in situ* (EIS). R was composed of initial scatter-hoarded seeds ($\mathrm{SH_I}$), seeds eaten after being removed (EAR) and missing seeds (M). $\mathrm{SH_I}$ was composed of the retained scatter-hoarded seeds (RSH) and total lost seeds (TL). $\mathrm{SH_I}$ indicated seeds removed from seed stations and scatter-hoarded by a rodent species. RSH indicated seeds initially scatter-hoarded and subsequently consumed or retained by cache owners by the end of the study period. RSH measured the reward of scatter-hoarding seeds to cache owners. TL indicated seeds not retained by cache owners but pilfered by conspecifics (CL), interspecifics (IL) or unidentified individuals (unknown loss, UL). Rodents also pilfered seeds (total pilferage, TP) scatter-hoarded by conspecifics (conspecific pilferage, CP) or interspecifics (interspecific pilferage, IP), and harvested seeds from unidentified individuals (unknown harvest, UH). Thus, the benefits that a rodent species gained from scatter-hoarding behavior of all rodent species were represented by the final scatter-hoarded seeds ($\mathrm{SH_F}$): $\mathrm{SH_F} = \mathrm{RSH} + \mathrm{TP} + \mathrm{UH}$. The benefits of rodents from non-scatter-hoarded seeds (NSH) were composed of seeds eaten *in situ* (EIS) and seeds eaten after being removed (EAR).

The scatter-hoarding preference (SHP) of a rodent

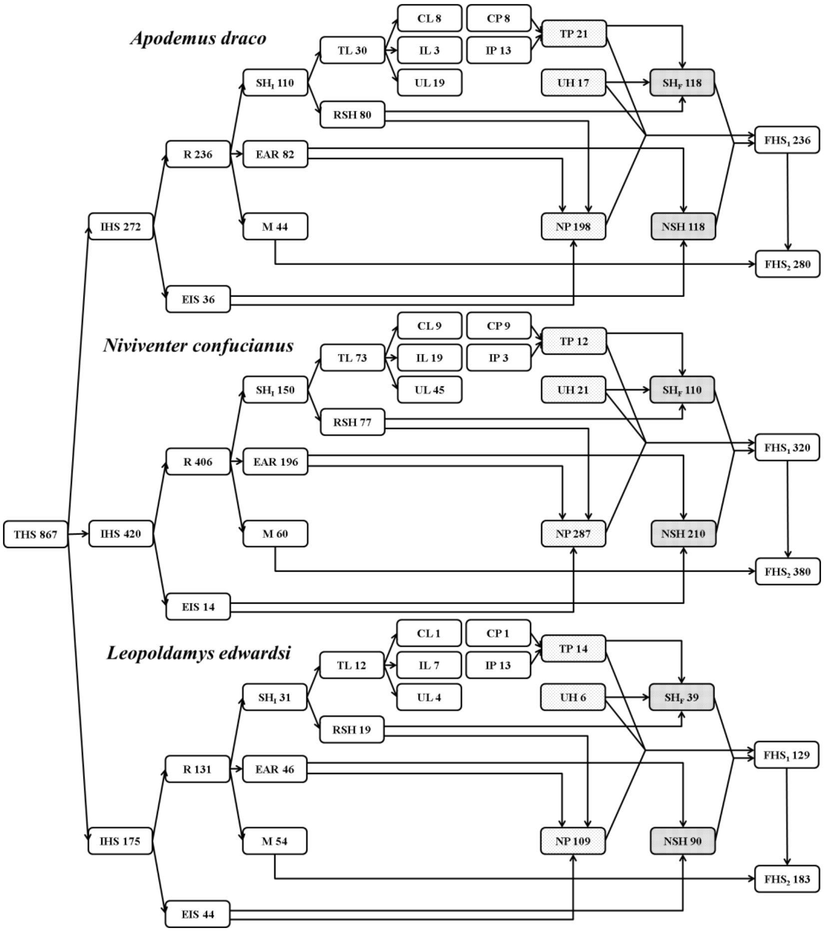

Figure 2 Seed fates of *Camellia oleifera* harvested by 3 sympatric rodent species in the field during 2013 to 2015. Numbers behind the parameters indicate the number of observed seeds with each seed fate. Dense stippled boxes indicate calculations of final harvested seeds (excluding missing seeds, i.e. $\mathrm{FHS_1}$) based on scatter-hoarded and non-scatter-hoarded seeds. Sparse stippled boxes indicate calculations of final harvested seeds (excluding missing seeds, i.e. $\mathrm{FHS_1}$) based on pilfered and non-pilfered seeds. THS = total harvested seeds; IHS = initial harvested seeds; R = removed seeds; EIS = seeds eaten *in situ*; $\mathrm{SH_I}$ = initial scatter-hoarded seeds; EAR = seeds eaten after being removed; M = missing seeds; TL = total loss of seeds; RSH = retained scatter-hoarded seeds; CL = conspecific loss of seeds; IL = interspecific loss of seeds; UL = unidentified loss of seeds; CP = conspecific pilfered seeds; IP = interspecific pilfered seeds; TP = total pilfered seeds; UH = unidentified harvested seeds; NP = non-pilfered seeds; $\mathrm{SH_F}$ = final scatter-hoarded seeds; NSH = non-scatter-hoarded seeds; $\mathrm{FHS_1}$ = final harvested seeds excluding missing seeds; $\mathrm{FHS_2}$ = final harvested seeds including missing seeds.

species was defined as: SHP = initial scatter-hoarded seeds (SH_I)/initial harvested seeds (IHS). We defined 4 criteria to measure the scatter-hoarding benefits (SHB) of a rodent species. SHB_1 = retained scatter-hoarded seeds (RSH)/initial scatter-hoarded seeds (SH_I). SHB_2 = final scatter-hoarded seeds (SH_F)/initial scatter-hoarded seeds (SH_I). SHB_3 = final scatter-hoarded seeds (SH_F)/final harvested seeds excluding missing seeds (FHS_1). SHB_4 = final scatter-hoarded seeds (SH_F)/final scatter-hoarded seeds including missing seeds (FHS_2).

We defined 3 criteria to measure the pilferage ability of a rodent species. Total pilferage ability (TPA) = total pilfered seeds of a rodent species/the sum of initial scatter-hoarded seeds of all 3 sympatric rodent species. The conspecific pilferage ability (CPA) = conspecific pilfered seeds of a rodent species/initial scatter-hoarded seeds of this species. The interspecific pilferage ability (IPA) = interspecific pilfered seeds of a rodent species/the sum of initial scatter-hoarded seeds of the other 2 rodent species.

We defined 2 criteria to measure the seed competition efficiency of a rodent species: initial competition efficiency (ICE) and final competition efficiency (FCE). ICE represents the seed harvesting efficiency of a rodent species during the pre-dispersal stage, and is the proportion of initial harvested seeds of a rodent species (IHS) in total harvested seeds of all 3 rodent species (THS), and weighted by the total biomass of this species. FCE represents the seed harvesting efficiency of a rodent species during the post-dispersal stage. FCE (FCE_1 or FCE_2) is the proportion of final harvested seeds of a rodent species (FHS_1 or FHS_2) in total harvested seeds of all 3 rodent species (THS), also weighted by the total biomass of this species.

Statistical analysis

All data analysis was conducted with R 3.3.1 (R Core Team 2016). Significant differences between proportions were tested using 2 × 2 Crosstabs and χ^2-tests with Yate's continuity correction, or Fisher's exact tests if the theoretical value was smaller than 5 (the significance level α was corrected from 0.05 to 0.0167 in interspecific pairwise comparisons). Pearson's correlation was used to test for significant correlations between scatter-hoarding benefits and scatter-hoarding preference. Kernel density estimation (KDE) was used to estimate the probability density of dispersal distances of 3 rodent species, and the kernel smoothing (ks) package in R 3.3.1 was used to estimate the percentages of the seeds dispersed by 3 rodent species within the searching radius of 30 m (Duong 2017).

RESULTS

Species composition and abundance of rodents

Three rodent species were captured in our experimental plot during the entire study (Table 1). Medium-sized *N. confucianus* ranked first in both trap success and total biomass, while large-sized *L. edwardsi* ranked second in total biomass and third in 2 trap success. Small-sized *A. draco* ranked third in total biomass and second in trap success.

Seed dispersal distance

The average primary dispersal distance of seeds dispersed by *A. draco*, *N. confucianus* and *L. edwardsi* was 4.3 ± 3.5, 7.4 ± 5.8 and 10.6 ± 8.4 m (mean ± SD), respectively. KDE analysis indicated that 100% of seeds harvested by *A. draco*, 99% of seeds harvested by *N. confucianus* and 96.4% of seeds harvested by *L. edwardsi* were within our searching radius of 30 m (Fig. 3). Large-sized rodent species dispersed seeds further than small-sized species.

Conspecific differences between cache retention and pilferage abilities

In the present study 2 × 2 Crosstabs and χ^2 analysis indicated that for each of the 3 rodent species, the cache retention ability (measured by SHB_1) was significant-

Table 1 Trap success and biomass of sympatric 3 rodent species during 2013 to 2015

Species	Number marked	Trap success[†] (%)	Total rodent biomass (g)	Average body mass (mean ± SD, g)
Apodemus draco	24 (15♂, 9♀)	0.69	538.0	22.42 ± 4.21
Niviventer confucianus	59 (37♂, 22♀)	1.49	4049.3	68.63 ± 22.49
Leopoldamys edwardsi	9 (4♂, 5♀)	0.16	2685.1	298.34 ± 117.14

[†] Total trap-nights = 7575.

ly higher than the total pilferage ability (TPA, measured by total pilferage rate; $P < 0.01$, Table 2). Over 50% of scatter-hoarded seeds were retained by cache owners by the end of the study period, while the total pilferage rate was less than 10% for all 3 species (Table 2).

Interspecific differences of scatter-hoarding preference, benefits and pilferage

IR camera footage indicated that among all the 1905 tagged seeds we placed, 1083 were harvested by rodents, and 822 seeds remained *in situ* for 2 weeks and were eventually retrieved by researchers; 216 of these harvested seeds were initially harvested by unknown individuals, and the remainder (867 seeds) was ascertained to be harvested by the 3 rodent species (THS). Among these 867 seeds, *N. confucianus* accounted for 48.4%, *A. draco* for 31.4% and *L. edwardsi* for 20.2% (Fig. 2). The scatter-hoarding preference (SHP, measured by rates of scatter-hoarding) of *A. draco* (40.44%) was greater than that of *N. confucianus* (35.71%), which was greater than that of *L. edwardsi* (17.71%) (Table 2). χ^2 analyses indicated that either *N. confucianus* or *A. draco* showed a significantly higher scatter-hoarding preference than *L. edwardsi* ($P < 0.01$). The scatter-hoarding benefits measured by proportion of retained scatter-hoarded seeds in initial scatter-hoarded seeds (SHB_1) of *A. draco* were significantly higher than that of *N. confucianus* ($P < 0.01$). The scatter-hoarding benefits measured by proportion of final scatter-hoarded seeds in final harvested seeds (SHB_3, SHB_4) of *A. draco* were significantly higher than those of *N. confucianus* and *L. edwardsi* ($P < 0.01$). These results indicated that the smaller *A. draco* showed a higher scatter-hoarding preference and scatter-hoarding benefits than the other 2 medium-sized or large-sized rodent species.

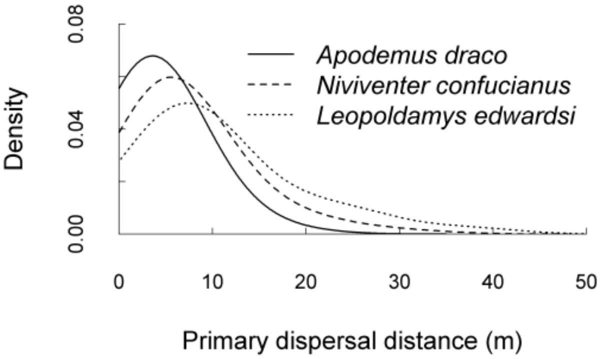

Figure 3 The kernel density estimation (KDE) curves of dispersal distance of the primary caches established by 3 rodent species.

Correlation analysis using the data in Table 2 indicated that during 2013 to 2015 the scatter-hoarding prefer-

Table 2 Estimation of the scatter-hoarding preference (SHP), scatter-hoarding benefits (SHB_1, SHB_2, SHB_3, SHB_4) and pilferage abilities (TPA, CPA, IPA) of 3 sympatric rodent species during 2013 to 2015

Year	Species	SHP	SHB_1	SHB_2	SHB_3	SHB_4	TPA	CPA	IPA
2013	Ad	52.34	65.67	1.04	67.96	53.44	8.03	5.97	10.00
	Nc	36.22	47.83	0.87	41.67	33.06	2.92	4.35	2.20
	Le	24.00	54.17	0.71	37.78	18.28	1.46	4.17	0.88
2014	Ad	6.12	—	—	16.98	16.36	5.95	—	6.17
	Nc	33.93	46.05	0.64	28.82	24.87	8.33	9.21	—
	Le	15.63	—	—	36.84	34.15	7.14	—	7.59
2015	Ad	42.11	82.50	0.98	48.75	41.49	7.14	10.00	3.33
	Nc	40.58	71.43	0.75	38.89	33.87	1.43	0.00	2.38
	Le	4.65	—	—	17.39	16.33	8.57	—	8.82
Total	Ad	40.44	70.00	1.07	50.00	42.14	7.22	7.27	7.18
	Nc	35.71	51.33	0.73	34.38	28.95	4.12	6.00	2.13
	Le	17.71	61.29	1.26	30.23	21.31	4.81	3.23	5.00

"—" represents no calculation data due to $n < 10$. Ad, *Apodemus draco*; CPA, conspecific pilferage ability; IPA, interspecific pilferage ability; Le, *Leopoldamys edwardsi*; Nc, *Niviventer confucianus*; TPA, total pilferage ability. For more details of the parameter definitions, see the text.

Table 3 Seed competition efficiencies of 3 rodent species at the pre-dispersal and post-dispersal stages

Species	IHS	FHS_1	FHS_2	ICE	FCE_1	FCE_2
Apodemus draco	272	236	280	505.6	438.7	520.4
Niviventer confucianus	420	320	380	103.7	79.0	93.8
Leopoldamys edwardsi	175	129	183	65.2	48.0	68.2

FHS1 and FHS2 indicate the final harvested seeds excluding or including missing seeds, respectively. FCE_1 and FCE_2 indicate the final competition efficiency excluding or including missing seeds, respectively. ICE, initial competition efficiency. HIS, indicates the initial harvested seeds. For more details of the parameter definitions, see the text.

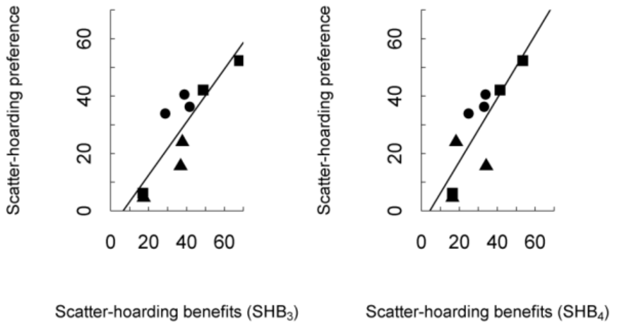

Figure 4 The relationship between scatter-hoarding preference (SHP) and scatter-hoarding benefits (SHB_3, left; SHB_4, right) of the 3 rodent species during 2013 to 2015. ■ = *Apodemus draco*, ◆ = *Niviventer confucianus*, ▲ = *Leopoldamys edwardsi*.

ence was significantly and positively correlated with the scatter-hoarding benefits (SHB_3: $P = 0.002$, SHB_4: $P = 0.006$; Fig. 4), and correlated with the SHB_2 ($P = 0.063$).

Interspecific differences in competition efficiency for seeds

Table 3 indicated that both of the initial competition efficiency (ICE) and the final competition efficiency (FCE) of small-sized *A. draco* were higher than those of the other 2 large-sized species (*N. confucianus* and *L. edwardsi*). Both of the ICE and FCE of medium-sized *N. confucianus* were higher than those of the largest species *L. edwardsi*.

DISCUSSION

Our results suggested that scatter-hoarding better rewarded cache owners, not pilferers. Scatter-hoarding could be an important strategy in food competitions among sympatric rodent species, particularly for small-sized species which have disadvantages in defending their larder caches against larger competitors. Specifically, by using a combination of the seed tagging and the IR camera tracking method, we found that all 3 rodent species showed high seed retention ability and low pilferage ability, and scatter-hoarding benefits were positively related to the degree of scatter-hoarding preference. We also found that small-sized *A. draco* showed higher scatter-hoarding preference, and gained higher benefits (or reward) from the scatter-hoarded seeds than medium-sized *N. confucianus* and large-sized *L. edwardsi*. Our study provided new insights into the evolution of scatter-hoarding behavior and mutualism between trees and rodents. We also provide a method for calculating the true interspecific and conspecific pilferage rates of small-sized seeds and rodents under field conditions.

Our results supported the pilferage avoidance hypothesis that scatter-hoarding strategy was adaptive because it could reduce the cache loss due to cache pilferage (Andersson & Krebs 1978; Stapanian & Smith 1978, 1984). This hypothesis was based on an assumption that scatter-hoarding cache owners were more likely to recover their own cached items than any other competitors, thereby repaying the efforts of scatter-hoarding (Andersson & Krebs 1978; Vander Wall & Jenkins 2003). Stapanian and Smith (1978) conducted field experiments to test their model for optimal spacing of scattered caches. In burial experiments, they artificially buried seeds of black walnuts (*J. nigra*) to simulate the natural caches made by squirrels, and then observed wild fox squirrels (*S. niger*) to take (pilfer) the buried seeds for 31 days. Their results showed the percentage of walnuts surviving from "pilferage" (not being pilfered, similar to SHB_1 in our study) could be as high as 87.5% (the average distance between adjacent seeds was 9.2 m), while the total pilferage rate was only 12.5%. Our study under field conditions showed that scatter-hoarding benefits (SHB_1) of all 3 rodent species was significantly higher than their total pilferage abilities (TPA), respectively, which was consistent with the pilferage avoidance hypothesis. Our results suggested that cache owners recovered the majority of their caches, and had greater reward from scatter-hoarding than pilferage. In fact, because occasionally the IR cameras failed to obtain, clear footage due to mechanical failure of the trigger, or the existence of the unmarked rodents in the experiment plot, SHB_1 was likely underestimated and some seeds counted as "unknown loss" (UL) could have been retrieved by cache owners.

Our results were not consistent with the reciprocal pilferage hypothesis that most scattered caches would be pilfered in a short period, leading to high levels of pilferage: up to 30% per day in some cases (Vander Wall & Jenkins 2003). In Jansen's study of Central American agoutis (*D. punctate*) in Panama, the majority (84%) of the agouti-cached seeds were pilfered while just 16% were recovered by cache owners (Jansen *et al.* 2012). However, in our study, we found that over 50% of scatter-hoarded seeds were retained by cache owners by the end of each tracking period (30 days), while the total pilferage rate was less than 10%. The variable results in the literature on the reward of scatter-hoarding for cache owners suggest that there were likely 2 opposite strategies of scatter-hoarding adopted by rodents: pilferage avoidance and reciprocal pilferage, depending on multiple conditions. One was the spatial-temporal condition. For example, in limited space such as in small experimental enclosures, the probability of random searching would be high, thus reciprocal pilferage would be the best strategy. Another condition was different rodent species composition among different studies. Their hoarding behavior and pilferage abilities may differ greatly. Seeds with strong odor or animals with strong olfactory capability may also correspond to an increased probability of seed pilferage. Usually, large seeds have a strong odor, particularly in wet conditions (Vander Wall 1998). In Jansen's study in Panama of the wet tropical rainforests, the seeds were quite large (10 g), which may have contributed to the observed high rate of pilferage. In a study by Yi *et al.* (2016b), seeds with a weak odor were more likely to be scatter-hoarded, while strong-smelling seeds were less frequently scatter-hoarded; chipmunks with artificially blocked olfactory capability showed a higher tendency for scatter-hoarding seeds. Some rodent species may be able to have a balance of scatter-hoarding or larder-hoarding based on the benefits of scatter-hoarding in different conditions. In our study, the tests were performed under field conditions, and the oil tea seeds were small (<2 g). Spatial memory would likely be important for rodents to find these scatter-hoarded seeds. Some rodents, especially cache owners, were found to relocate their caches in a direct way (without sniffing around and searching hard), probably by using spatial memory, while pilferers which were prone to investigate before pilferage probably relied on olfactory clues. By referring to previous methods (Hirsch *et al.* 2013), we found that the frequency of investigation behaviors (including sniffing and circling around the cache) before cache relocation of cache owners (34.5%, $n = 29$) was significantly lower than that of pilferers (76%, $n = 25$) ($\chi^2 = 7.71$, $P = 0.005$). This observation indicated that spatial memory could explain why scatter-hoarding provided a better reward for cache owners. As was shown in previous studies, cache owners of some species, such as eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788) (Jacobs & Liman 1991; Steele *et al.* 2011), fox squirrels (Lavenex *et al.* 1998), yellow pine chipmunks [*Tamias amoenus* (J. A. Allen, 1890)] (Vander Wall *et al.* 2008) and Siberian chipmunks [*Tamias sibiricus* (Laxmann, 1769)] (Yi *et al.* 2016a; Zhang *et al.* 2016a), had advantages in retrieving their own caches over pilferers with the aid of spatial memory.

If scatter-hoarding offers a better reward for cache owners, it may play a significant role in food competition among sympatric rodent species, and would contribute to explaining their coexistence. In our study, we found that *A. draco* showed higher scatter-hoarding preference than the other 2 species. *A. draco* is much smaller in size than *N. confucianus* or *L. edwardsi*. Usually small-sized animals would face a disadvantage in food competition when encountering larger animals. Indeed, large rodents like *N. confucianus* or *L. edwardsi* showed dominance over the small-sized *A. draco* in both enclosure and field tests (personal observations). To overcome this disadvantage of direct competition, small-sized animals need to improve their food foraging efficiency per unit biomass. As for the interspecific pilferage abilities, *A. draco* pilfered 7 seeds from *N. confucianus* and 6 seeds from *L. edwardsi*; *N. confucianus* pilfered 2 seeds from *A. draco* and one seed from *L. edwardsi*; *L. edwardsi* pilfered one seed from *A. draco* and 12 seeds from *N. confucianus*. Small-sized *A. draco* seemed to have higher interspecific pilferage ability than the other 2 species. This needs further investigation due to the small sample size of interspecific pilfered seeds. In our study, we found that small-sized *A. draco* showed a higher scatter-hoarding preference, retention ability and reward from scatter-hoarding seeds, and also higher competition efficiency per unit biomass for seeds under field conditions.

It should also be pointed out that our methods still had some limitations. Occasional mechanical failure of the cameras and the appearance of unmarked rodents in the study plot could lead to some unidentified seed fates or dispersers, and, finally, result in lower estimation of some criteria such as RSH, CL, IL. However, our methods still enabled us to reveal the seed retention and pilferage abilities of small-sized rodents directly, and allowed us to evaluate the benefits or losses of scatter-hoarded seeds, as well as to discuss the role of scatter-hoarding in food competition and species coexistence of rodents in forest ecosystems. In future, we should improve rodent-seed tracking technology to determine the final fate of the cached seeds, and to study the competition of multiple seed species with different odor levels pre-evaluated in different natural rodent communities, and to reveal the mechanisms of seed hoarding, food competition and species coexistence.

Our study implied that scatter-hoarding showed more benefits to the cache owners, not the pilferers. It is obvious that such a natural selection at the individual level is the driving force in the formation of mutualism between tree and rodent species. Our study also revealed that scatter-hoarding preference varied among species and years, which were determined by the scatter-hoarding benefits. Such a difference in scatter-hoarding preference would significantly change the species interactions and the contribution to seed regeneration in natural conditions. Besides, our study showed that more capable scatter-hoarders had better performance in competing for seeds, which would, in turn, facilitate the dispersal of plant seeds. This fact thereby proved the significant role of scatter-hoarding in maintaining species coexistence and seedling regeneration of many tree species. Therefore, scatter-hoarders should be carefully monitored and managed.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found in the online version of this article at the publisher's website.

Figure S1 The arrangement of live traps and seed stations. □ denotes a live trap, and ○ denotes the location of a seed station.

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