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Original Article

Risk of cache pilferage determines hoarding behavior of rodents and seed fate

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Cache pilferage by competitors is thought to drive the evolution of hoarding behavior in animals, which plays significant roles in tree regeneration and formation of mutualisms between trees and animals. However, little is known how cache pilferage risk among seeds of different tree species or years affects hoarding behavior and seed dispersal by animals. We hypothesized that scatter-hoarding rodents could adjust hoarding behavior according to variation in cache pilferage risk among seeds and years to minimize cache pilferage, by investigating the relationship between cache pilferage risk and seed dispersal of 7 tree species over 3 years in tropical forest in southwest China. Among years, the high pilferage risk was related to high probability of larder-hoarding and short periods of scatter-hoarding; whereas, the probability of scatter-hoarding was higher in intermediate pilferage year than in both low and high pilferage years. Among seeds, high pilferage risk was related to low probability and short periods of scatter-hoarding. Our results indicated that cache pilferage risk significantly affected hoarding behaviors and seed dispersal by scatter-hoarding rodents as well as seed fates. Cache pilferage risk was a reliable explanatory factor for variation in seed dispersal, and it might be an important driving force in the evolution of rodent hoarding behaviors and seed characteristics.

Key words: **cache pilferage risk, hoarding behavior evolution, larder-hoarding, scatter-hoarding, seed dispersal, survival time.**

INTRODUCTION

Food hoarding is a widespread behavior adopted by many animals to survive food shortage periods, which can play a significant role in seedling regeneration and formation of mutualisms between plants and animals in forest ecosystems (Howe and Smallwood 1982; Vander Wall 1990). However, many studies have reported that seeds cached by food-hoarding animals are frequently pilfered by competitors (Clarke and Kramer 1994a, b; Dally et al. 2006; Vander Wall et al. 2006; Jansen et al. 2012), and pilferage rates is often high (varying from 2% to 30% per day) (see review by Vander Wall and Jenkins 2003). Furthermore, cache pilferage cannot be avoided or prevented by most animals. Thus, the primary task for seed hoarders is to keep pilferage at an acceptable level to make food hoarding profitable (Vander Wall and Jenkins 2003).

Vander Wall and Jenkins (2003) suggested that some small animals with overlapping home ranges are able to tolerate high pilferage levels. They proposed a hypothesis, termed the Reciprocal Pilferage Theory, which states that cache pilferage is not equal to cache loss as thieves usually steal foods and cache them elsewhere that can be retrieved by the original food hoarders. In another study, Huang et al. (2011) reported that scatter-hoarding rodents

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were able to tolerate high pilferage by enhancing cache frequency. However, several previous studies have demonstrated that food-hoarding animals have evolved a series of strategies to reduce cache pilferage, such as by adjusting consumption and caching rates, repeatedly recovering and moving hoards, aggressively defending caches, switching from scatter- to larder-hoarding, delaying caching in the presence of potential thieves, and spacing caches farther apart or placing them out of sight (see review by Dally et al. 2006). Most studies have primarily focused on food-hoarding birds. Recently, an increasing number of studies have found that scatter-hoarding rodents can move seeds to specific habitats or microsites (e.g., open areas) to reduce cache pilferage (Munoz and Bonal 2011; Steele et al. 2014; Steele et al. 2015). Agoutis *Dasyprocta punctata* have been shown to disperse seeds into areas with a low density of conspecific trees (Hirsch et al. 2012), and kangaroo rats *Dipodomys merriami* have been observed spacing seeds at an optimal density (Daly et al. 1992; Jenkins et al. 1995) to reduce cache pilferage. These studies indicate that scatter-hoarding rodents have evolved strategies to reduce cache pilferage when they hoard foods. Thus, cache pilferage by competitors is considered as an important driver of hoarding behavior evolution in these animals (Smith and Reichman 1984; Vander Wall and Jenkins 2003).

Rodent hoarding behavior on plant seeds may differ greatly among rodent species (Hollander and Vander Wall 2004; Zhang et al. 2016), plant species (Forget et al. 1998; Xiao et al. 2006b), and years (Vander Wall 2002; Jansen et al. 2004). Seed traits (e.g. nutrient content, seed size, tannin content, seed coat thickness, and seed perishability), and the relative abundance between seeds and seed consumers usually have been considered as the primary factors explain these differences, however, their conclusions are often inconsistent (see review by Lichti et al. 2017). In present study, we predicted that variation in cache pilferage risk among seed species and years might be an alternative possible explanatory factor of this phenomenon, as variation in cache pilferage risk among seeds and years are likely to be caused by both the differences in seed characteristics among species and the variations of seed and predator abundance among years (Moore et al. 2007; Hollander et al. 2012). Thus, we predict that cache pilferage risk is a reliable proxy factor and that whether a food-hoarding animal undertakes a strategy of seed caching is affected by its probability of being able to reduce cache pilferage. To the best of our knowledge, few studies has quantitatively evaluated the relationship between cache pilferage risk among different seed species (or years) and seed dispersal or hoarding behavior of rodents.

In this study, we predicted that scatter-hoarding rodents could adjust hoarding behavior according to the variation in cache pilferage risk (defined as the probability of cache pilferage per day) among plant species and years to minimize cache pilferage. Increasing consumption and reducing caching rates, quickly recovering and consuming hoards may make seed hoarders get more foods when risk of cache pilferage was high (Dally et al. 2006). Meanwhile, switching hoarding behavior from scatter- to larder-hoarding may help to reduce cache pilferage when risk of cache pilferage of scatter-hoarding is high (Dally et al. 2006). Thus, we made the following 2 hypothesis: 1) the probability of scatter-hoarding would be lower and the survival time of scatter-hoarded seeds shorter in years or for seed species with a higher pilferage risk, and vice versa. 2) Variation in cache pilferage risk among seeds or years would result in a transition between scatter- and larder-hoarding behaviors; specifically, larder-hoarding by rodents would be more common in years or for seed species with a higher pilferage risk, and vice versa.

We investigated the relationship between cache pilferage risk and seed dispersal of 7 tree species across 3 years in the Xishuanban tropical forests, Yunnan Province, China. We estimated seed cache pilferage risk for tree species by investigating the pilferage rate of the artificial caches, and we investigated the dispersal of these seeds with seed releasing and tracking experiments. Then, we analyzed the relationships between cache pilferage risk and seed dispersal parameters (including the probability of scatter-hoarding, probability of larder-hoarding, and survival time of scatter-hoarded seeds).

MATERIAL AND METHODS

Study site and species

This study was conducted in a tropical, montane, evergreen broad-leaved forest, in Menglun Nature Reserve, Xishuangbanna, Yunnan Province, China (21°50′N , 101°12′E, elevation 760 m). The forest was dominated by *Castanopsis echidnocarpa*, *Aporosa yunnanensis*, *Olea rosea*, *Lithocarpus truncates*, and *Schima wallichii* (Zhang and Cao 1995). Seeds of 7 tree species in the family Fagaceae were studied: *C. echidnocarpa*, *C. calathiformis*, *C. hystrix*, *C. mekongensis*, *Quercus acutissima*, *L. truncates*, and *L. leucostachyus*. These species are either dominant or common species in the tropical evergreen broad-leaved forest in Xishuangbanna (Zhu 2006). The characteristics of these seeds varied among species (Supplementary Table S1, and see a discussion in Wang et al. 2014). Previous studies have found that Chinese white-bellied rats (*Niviventer confucianus*) are the most abundant rodent species, and red spiny rats (*Maxomys surifer*), chestnut rats (*N. fulvescens*), and yellow-bellied rats (*Rattus flavipectus*) are commonly seen within the experimental stands (Cao et al. 2011; Wang et al. 2014; Cao et al. 2016, 2017). Chinese white-bellied rats and chestnut rats showed both scatter- and larder-hoarding behavior, red spiny rats showed predominantly scatter-hoarding behavior, whereas yellow-bellied rats showed predominantly larder-hoarding behavior (Wang et al. 2014; Geng et al. 2017).

Seed releasing and tracking experiments

Seeds of 7 common species from the Fagaceae family (*C. echidnocarpa*, *C. calathiformis*, *C. hystrix*, *C. mekongensis*, *L. leucostachyus*, *L. truncates*, and *Q. acutissima*) were used in seed releasing and tracking experiments from December 2010 to December 2013. Ten seed stations 20–50 m apart were set up along a single transect. Twenty tagged seeds for each species were placed at each station. In total, 1400 seeds were used in this experiment each year. Tagged seeds at each seed station were covered using a steel mesh enclosure (1.0 × 1.0 × 0.5 m, mesh size 1 × 1 cm) with one small hole (10 × 10 cm) on each of the 4 walls to allow access by small rodents but prevent entrance by large vertebrates, e.g. the wild boar, *Sus scrofa*. Seeds were marked by attaching a small coded plastic tag to each seed by a thin steel thread as has been done in other studies (Zhang and Wang 2001; Xiao et al. 2006a). Plastic tags have a negligible effect on seed removal (Xiao et al. 2006a).

Tagged seeds were surveyed at days 1, 4, 7, 14, and 28 to determine their status and were categorized as intact, predated, or removed. During each survey, we intensively searched the area within a 40-m radius around each seed station to retrieve the removed seeds and record the seed fates. For each survey, 3 people searched the entire area independently, but concurrently. Seeds that removed from seed stations were categorized as scatter-hoarded (buried in the surface soil or beneath leaf litter), larder-hoarded (seeds that were found hoarded in the underground burrows or tree cavities by checking underground burrows or trees cavities when we searched for removed seeds), predated, or missing (not located due to a visual barrier or more likely to being larder-hoarded in burrows or tree cavities). We also recorded the dispersal distances of cached seeds from the source seed station. Cached seeds were marked using a numbered bamboo stick so that they could be relocated. At subsequent visits, we checked for cached seeds until they were recovered (eaten or removed) by animals. If a marked cache was removed, the area around the cache was extensively searched in an attempt to relocate the seeds.

The plastic tags might make the caches a little more conspicuous to prospective pilferers. However, we did not think that this issue could significantly influence our results, as we were interested in the pilferage difference among different plant species of seeds, and the effect of plastic tag on pilferage should be equal to all the seeds.

Estimation of pilferage risk from artificial caches

Artificial caches were used to estimate cache pilferage risk. Cache pilferage rates were measured by burying seeds under leaf litter and beneath shrubs to simulate caches made by rodents. Sixteen (in 2010) or 14 (in 2011–2013) parallel transects (spaced 10 m apart, about 100 m away from the nearest seed releasing stations, see Seed releasing and tracking experiments) were set up to bury seeds under leaf litter (~5 mm) simulating caches made by rodents (more than 80% of the scatter-hoarded seeds were buried under leaf litter by rodents in our study sites). Along each parallel transect, there were 35 artificial caches, spaced 4 m apart. Each cache was a different seed starting with *C. echidnocarpa* and proceeding in order *C. calathiformis*, *C. hystrix*, *C. mekongensis*, *Q. acutissima*, *L. truncates*, and *L. leucostachyus* (same species used in the seed releasing and tracking experiments), then starting a new cycling around after *L. leucostachyus*. In total, 560 (2010) and 490 (2011–2013) artificial caches were made each year, and 80 (2010) or 70 (2011–2013) for each species per year. The density of our simulated caches was a little lower than what naturally occurred for small-seeded species (e.g. *C. echidnocarpa*, *C. calathiformis*, and *C. hystrix*, with a mean dispersal distance from 3 to 8 m, see Cao 2009), but was a little higher than what naturally occurred for large-seeded species (e.g. *C. mekongensis* and *Q. acutissima*, with a mean dispersal distance from 10 to 21 m). Each artificial cache was labeled using a 30-cm branch (about 0.5–0.8 cm in diameter) inserted into the soil 12 cm away from the cache, and a small plastic tag was tied to a shrub 1 m above the cache. These labels were set up at least one week prior to the experiments. Artificial caches were observed at 1, 4, 7, 14, and 28 days after being presented, and seeds pilfered were recorded. Pilfered seeds included seeds predated (seed fragments were found at artificial cache sites) or removed away (seeds disappeared) by rodents. To avoid disturbance related to human odor, disposable PVC gloves were worn during the whole process.

Data analysis

Only 3 seeds were eaten and no seeds were removed within 28 days in 2012 because of the mast-seeding phenomenon of *C. echidnocarpa* (see Appendix S1). Thus, we only analyzed data from the other 3 years (2010, 2011, and 2013).

In the artificial cache pilferage experiments, the proportion of the caches pilfered on the 14th day for each species in each year was used to assess cache pilferage risk for different seeds among years because 14 days was close to the mean seed survival time of scatter-hoarded seeds (ranging from 5 to 18 days for different plant species among the 3 years). In the seed releasing and tracking experiment, the data collected before day 28 were used for analysis because most seeds (including cached seeds) were consumed by this day.

Variations in the proportion of caches pilferage on the 14th day among years and species were analyzed by generalized linear mixed models (GLMMs), whereas year and seed species were treated as fixed variables and parallel transect (used to set up artificial caches) as the random variable. The sampling unit was the proportion of seeds pilfered in a transect for one plant in each year, modeled as a binomial distribution with a logit-link function (Bolker et al. 2009).

Variations in the probability of scatter-hoarding and larder-hoarding (with a binomial distribution and logit-link function) among years and species were similarly analyzed using GLMM, whereas year and seed species were treated as fixed variables and seed station were treated as random variables. The sampling unit was the proportion of seeds scatter-hoarded or larder-hoarded in a seed station for one plant in each year, modeled as a binomial distribution with a logit-link function. Variation in mean seed survival time of scatter-hoarded seeds (these data were log transformed to meet normal distribution) among years and species were analyzed by linear mixed models (LMMs), whereas years and seed species were treated as fixed variables and seed station was treated as random variable. The sampling unit is individual seed (scatter-hoarded seeds). The Tukey method was applied for post hoc pair-wise comparison between years or species.

GLMMs were used to test the relationship between cache pilferage risk and the probability of scatter-hoarding and larder-hoarding (with a binomial distribution and logit-link function) among species in different years with seed stations as random variables. Because of the limited sample size, we did not analyze the relationship between cache pilferage risk and the probability of larder-hoarding in 2011. LMMs were used to test the relationship between cache pilferage risk and seed survival time of scatter-hoarded seeds (these data were log transformed to meet normal distribution) in different years with seed stations as random variables.

GLMM and LMM were applied by *lme4* package in R (R, version 3.4.0; R Development Core Team 2017), and the Tukey method was applied by *lsmeans* package in R. Analysis of Variance with Wald Chi-square tests or F-tests were performed for testing the significance of fixed categorical variables in GLMMs and LMMs using *Anova* function in *car* package of R software.

RESULTS

Variation in cache pilferage risk

We found that cache pilferage in simulated cache experiments was significantly different among years (x^2 = 98.7, $P < 0.001$, Table 1) and species (x^2 = 22.3, $P = 0.001$, Table 1). Cache pilferage in 2010 (2.0% ± 0.24 per day, mean ± SE, defined as a high pilferage year, Figure 1a) was significantly higher than it was in 2011 (0.2% ± 0.06 per day, defined as a low pilferage year; Tukey method, $P < 0.001$) and 2013 (1.0% ± 0.09 per day, defined as an intermediate pilferage year; Tukey method, $P < 0.001$), and mean cache pilferage in 2013 was also significantly higher than it was in 2011 (Tukey method, $P < 0.001$). Variation in cache pilferage among years was similar for all 7 species (Supplementary Figure S1a).

Variation in postremoval seed fates among years

The probability of scatter-hoarding, larder-hoarding, and survival time of scatter-hoarded seeds varied greatly among years (all $P < 0.001$; Table 1).

There was a transition between scatter- and larder-hoarding among the 3 years. The probability of scatter-hoarding in the high (2010) and low (2011) pilferage year was significantly lower than in the intermediate pilferage year (Tukey method, all $P < 0.01$, Figure 1b). Although the probability of larder-hoarding in the high pilferage year (2010) was significantly higher than it was in the low (2011, Tukey method, $P < 0.001$, Figure 1c) and intermediate pilferage year (2013, Tukey method, $P < 0.001$, Figure 1c).

Table 1

The summary of the GLMMs or LMMs analyzing the variation of the proportion of caches pilferage and postdispersal seed fates among years and species

	Wald Chi-square or F-tests	
	x^2	P
Caches pilferage		
Year	98.7	<0.001
Species	22.3	0.001
Scatter-hoarding		
Year	16.8	<0.001
Species	350	<0.001
Larder-hoarding		
Year	111.3	<0.001
Species	124.1	<0.001
Seed survival time		
Year	494	<0.001
Species	84.1	<0.001

Analysis of Variance with Wald Chi-square tests or F-tests are performed for testing the significance of fixed categorical variables (year and species) in GLMMs and LMMs using *Anova* function in *car* package of R software.

Mean seed survival time of scatter-hoarded seeds in the low pilferage year (2011) was significantly longer than in high (2010, Tukey method, $P < 0.001$; Figure 1d) and intermediate (2013, Tukey method, $P < 0.001$; Figure 1d) pilferage years; and the mean survival time of scatter-hoarded seeds in the intermediate pilferage year was also significantly longer than it was in high pilferage year (Tukey method, $P < 0.001$).

Furthermore, we found that variation in scatter-hoarding, larder-hoarding, and seed survival time of scatter-hoarded seeds was similar among years for most species (Supplementary Figure S1b–d).

Relationship between cache pilferage risk and postremoval seed fates among species

The probability of scatter-hoarding, larder-hoarding, and the survival time of scatter-hoarded seeds varied greatly among species (all $P < 0.01$, Table 1).

The probability of scatter-hoarding was lower for species with high cache pilferage risk in 2011 ($R^2 = 0.4$, $z = -9.1$, $P < 0.001$, Figure 2b and Table 2) and 2013 ($R^2 = 0.13$, $z = -9.5$, $P < 0.001$, Figure 2c), but not in 2010 ($R^2 = 0.004$, $z = -0.4$, $P = 0.696$, Figure 2a). There was an inconsistent pattern in the relationship between cache pilferage risk (among species) and the probability of larder-hoarding among different years. The probability of larder-hoarding was higher for species with a high pilferage risk in 2010 ($R^2 = 0.05$, $z = 5.5$, $P < 0.001$, Figure 2d and Table 2), but was lower for species with a high pilferage risk in 2013 ($R^2 = 0.134$, $z = -4.2$, $P < 0.001$, Figure 2f).

Seed survival time of scatter-hoarded seeds was shorter for species with high cache pilferage risk in all 3 years (all $P < 0.001$, Figure 3 and Table 2).

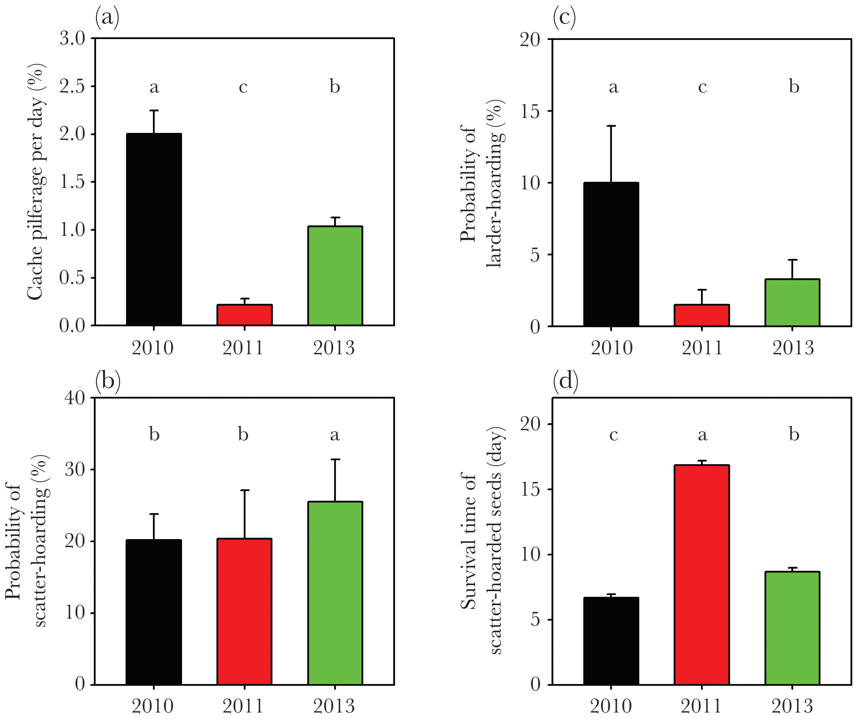

Figure 1

Variation in (a) the probability of cache pilferage per day (mean of 7 species, mean ± SE), (b) the probability of scatter-hoarding, (c) probability of larder-hoarding, and (d) survival time of scatter-hoarded seeds for 3 years. Different letters indicate significant differences among years ($P < 0.05$).

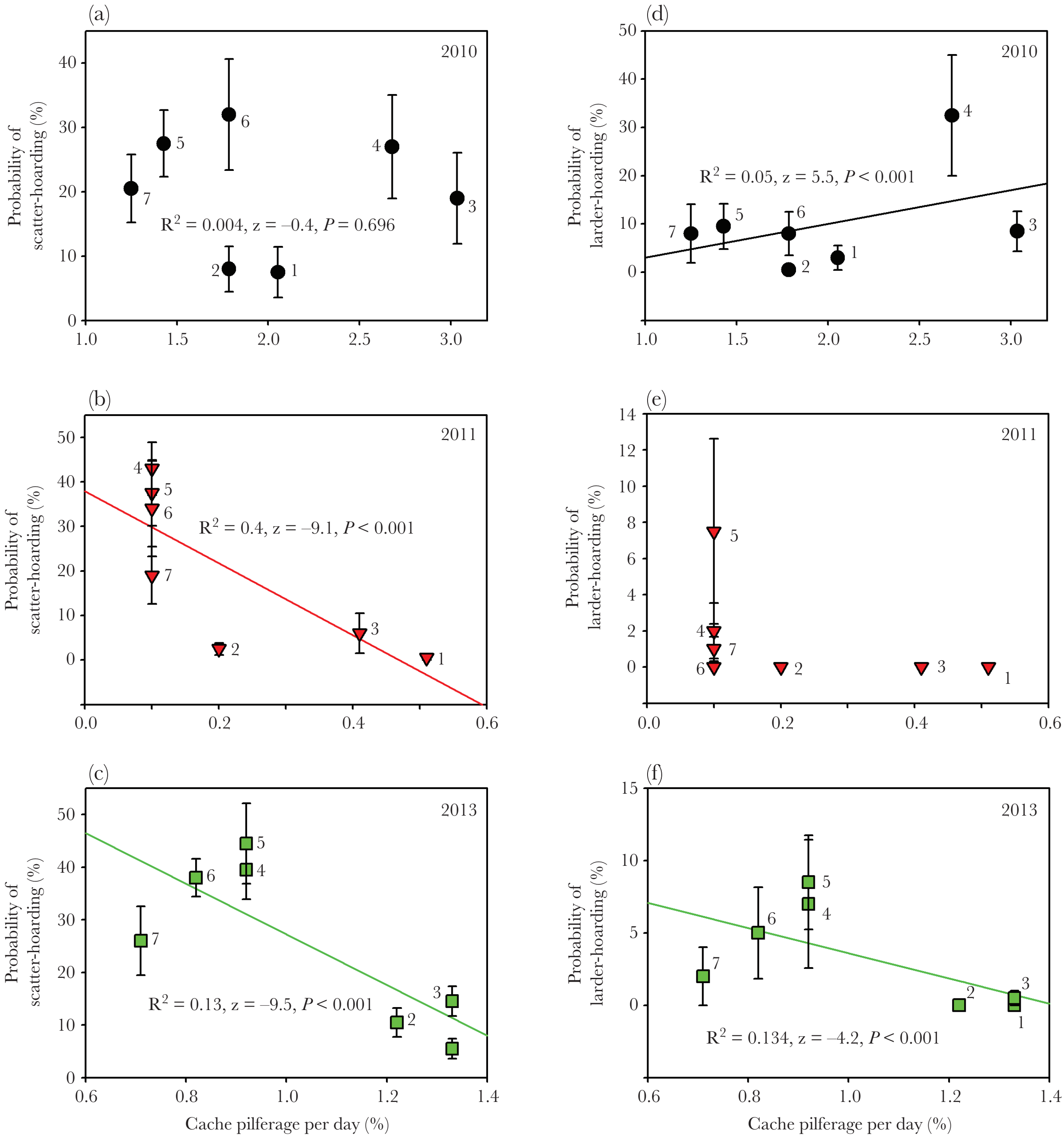

Figure 2

Relationships between cache pilferage risk (among seed species) and the probability of scatter-hoarding (a, b, and c) or larder-hoarding (d, e, and f) in 3 years (the trend line was added by simple linear regression). Numbers represent plant species: 1, *Castanopsis echidnocarpa*; 2, *Castanopsis calathiformis*; 3, *Castanopsis hystrix*; 4, *Castanopsis mekongensis*; 5, *Quercus acutissima*; 6, *Lithocarpus truncates*; and 7, *Lithocarpus leucostachyus*.

DISCUSSION

Previous studies have demonstrated that seed-hoarding animals exhibited behaviors to reduce risk of cache pilferage by competitors; however, to date, no study has quantitatively evaluated the relationship between cache pilferage risk among seed species (or years) with seed dispersal or hoarding behavior of rodents. Our results indicated that variations in cache pilferage risk among seeds and years could be a proxy of variations of both seed characteristics and abundances of seeds and rodents, which could better explain the variations in seed fates and rodent hoarding behaviors. Our results suggested that scatter-hoarding rodents might adjust seed dispersal and hoarding behavior according to variation in cache pilferage risk among seed species and years. Specifically, scatter-hoarding rodents preferred to eat unsafe seeds (those with a high risk of pilferage) and scatter-hoard safe seeds (those with a low risk of pilferage). In addition, scatter-hoarding rodents switched their behavior from scatter- to larder-hoarding in the year when cache pilferage was high. Among seeds that were scatter-hoarded, safe seeds in the caches survived longer than unsafe ones. Furthermore, scatter-hoarded seeds survived longer in safe years than in unsafe

Table 2

The summary of the GLMMs or LMMs analyzing the relationship between cache pilferage risk and the probability of scatter-hoarding, larder-hoarding, and survival time of scatter-hoarded seeds among species in 3 years

Year	Variables	Estimate ± SE	*z*/*t**	*P*
Scatter-hoarding				
2010	(Intercept)	−1.5 ± 0.37	−4.0	<0.001
	Cache pilferage	−0.04 ± 0.11	−0.4	0.696
2011	(Intercept)	0.19 ± 0.28	0.7	0.485
	Cache pilferage	−10.74 ± 1.18	−9.1	<0.001
2013	(Intercept)	1.69 ± 0.31	5.4	<0.001
	Cache pilferage	−2.79 ± 0.29	−9.5	<0.001
Larder-hoarding				
2010	(Intercept)	−5.28 ± 0.83	−6.4	<0.001
	Cache pilferage	0.87 ± 0.15	5.5	<0.001
2011	(Intercept)	—	—	—
	Cache pilferage	—	—	—
2013	(Intercept)	−1.43 ± 1.09	−1.3	0.191
	Cache pilferage	−3.49 ± 0.83	−4.2	<0.001
Seed survival time				
2010	(Intercept)	0.87 ± 0.07	12.1	<0.001
	Cache pilferage	−0.08 ± 0.02	−3.8	<0.001
2011	(Intercept)	1.36 ± 0.02	65.2	<0.001
	Cache pilferage	−1.48 ± 0.13	−10.8	<0.001
2013	(Intercept)	1.18 ± 0.08	14.4	<0.001
	Cache pilferage	−0.37 ± 0.08	−4.5	<0.001

The proportions of cache pilferage were treated as fixed variables and seed stations as random variables in all of the models.
*‘*z*’ is from significant effects of GLMMs with binomial distribution, and ‘*t*’ from that of LMMs with Gaussian distribution.

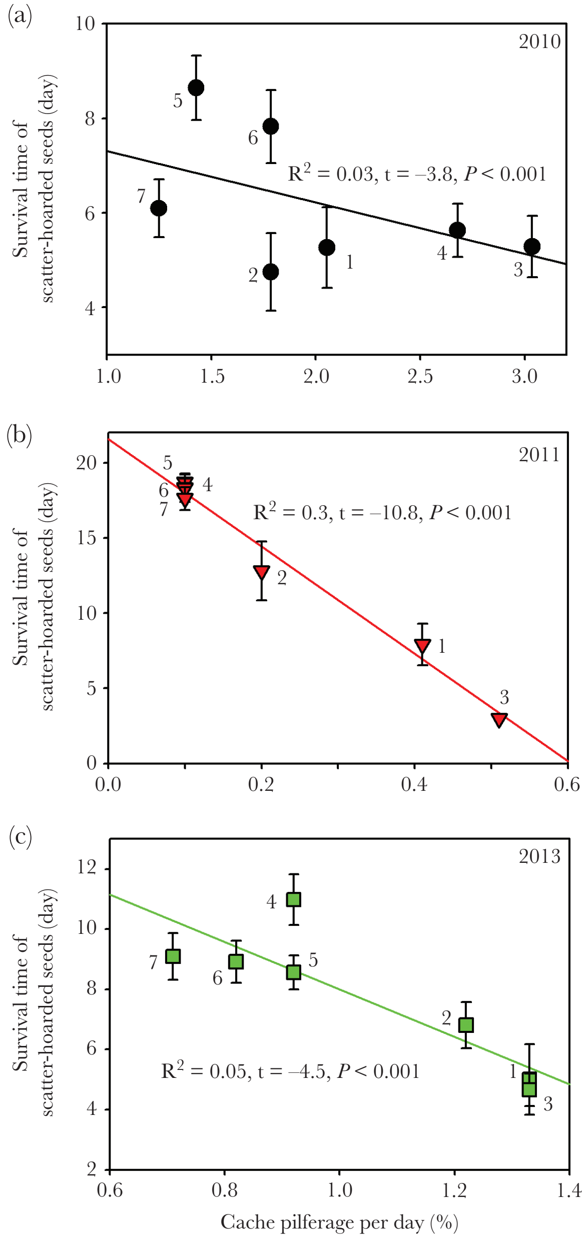

Figure 3
Relationships between cache pilferage risk (among seed species) and survival time of scatter-hoarded seeds in caches in 3 years (the trend line was added by simple linear regression). Numbers represent plant species: 1, *Castanopsis echidnocarpa*; 2, *Castanopsis calathiformis*; 3, *Castanopsis hystrix*; 4, *Castanopsis mekongensis*; 5, *Quercus acutissima*; 6, *Lithocarpus truncates*; and 7, *Lithocarpus leucostachyus*.

years. These results indicated that rodents preferred to recover and consume the unsafe seeds quickly, and preferred to recover and consume their hoarded seeds more quickly in years with higher risk of cache pilferage. Some of the cached seeds might be pilfered by competitors. However, both the low pilferage rate (varied from 0.2% to 2.0% among years, Figure 1a) and short seed survival time of scatter-hoarded seeds (varied from 6.2 to 13.8 days, Figure 1d), suggested that most of the cached seeds were recovered by cached owners. These strategies may be important to scatter-hoarding rodents that can recover many of their own caches and continue to hoard food to ensure long-term survival and reproduction.

We found that cache pilferage risk varied greatly among seeds. Hollander et al. (2012) found a similar pattern when comparing pilferage rate between wildland and cultivated seeds. Yi et al. (2016) reported that the strength of the seed odor significantly affects cache pilferage risk by scatter-hoarding rodents. However, the components of seed odor vary greatly among seeds, and it is difficult to distinguish (Jorgensen 2001). It is logical that seeds with stronger seed odor may be more easily discovered by other rodents. Nevertheless, perception of the presence of seeds is not equal to pilferage. Previous studies have found that the time the seeds remain at artificial seed stations varies greatly among seeds, and rodents did not predate or remove seeds of some species after encountering them (Xiao et al. 2006b; Zhang and Zhang 2008; Wang et al. 2013), e.g. most low-tannin seeds were predated or removed by rodents within 3 days, but high-tannin seeds remained for several weeks at the same seed station (Xiao et al. 2008). Vander Wall (2010) suggested that plants had evolved strategies to reduce cache pilferage risk. We propose that chemical or physical defenses that have been evolved to escape animal predation may also help to reduce cache pilferage. We did find that high tannin seeds (e.g. *Q. acutissima*) and seeds with thick coats (e.g. *C. mekongensis*) were typically safe (had a lower cache pilferage risk) and had higher seed survival; on the contrary, low-tannin seeds or seeds with thin coats were typically unsafe (Supplementary Figure S1; see a discussion of seed characteristics in Wang et al. 2014). However, the effects of chemical and physical defenses on cache pilferage need further investigation.

The results showed that cache pilferage risk varied greatly among years. This may be caused by variation in both seed abundance and rodent density among years while high cache pilferage risk may related to low seed abundance and high rodent density (see

Appendix S1), and vice versa. Here we found that scatter-hoarding rodents switched their behavior from scatter- to larder-hoarding in the year when cache pilferage was high, and high pilferage risk was also related to short periods of scatter-hoarding. Seed abundance fluctuation has also been used to explain variation in seed fate and hoarding behavior among years, but the conclusions drawn are often inconsistent (Vander Wall 2002; Jansen et al. 2004; Xiao et al. 2013; Cao et al. 2017). Our results indicated that variation in cache pilferage risk among years could be a proxy of variations in seed and rodent abundances, which could better explain the variations of seed fates and rodent hoarding behavior among years.

Our results demonstrated that the hoarding strategies of rodents were adjusted based on the risk of cache pilferage. Changes of rodent community composition might be a possible explanation. However, we found *N. confucianus* was the only predominant species across all years (see Appendix S1). And *N. confucianus* showed both scatter- and larder-hoarding behavior (Cao et al. 2011; Wang et al. 2014). Thus, it was likely that variation of probability of larder-hoarding among years was caused by the changes of hoarding behavior of *N. confucianus* based on the variation of cache pilferage risk. Vander Wall et al. (2009) found that ground squirrels make large, deep caches and larder-hoard most seeds to avoid pilferage from chipmunks; in contrast, chipmunks make small, shallow caches as ground squirrels cannot detect and remove these caches easily. Some other studies have found similar results that, in order to reduce pilferage of their reserve, rodents usually hoard their seeds in low densities (Daly et al. 1992; Jenkins et al. 1995) and select an area as the caching site where a pilferer could not find the hoarded seeds (Munoz and Bonal 2011; Hirsch et al. 2012; Steele et al. 2014). It seems that scatter-hoarding rodents have evolved a series of strategies to reduce cache pilfering. Our findings support the previous hypothesis that cache pilferage by competitors could be a driving force in the evolution of hoarding behavior of animals (Smith and Reichman 1984; Vander Wall and Jenkins 2003).

Our study indicated that whether a seed would be scatter-hoarded and used as a long-term reserve may be affected by whether the seed was safe to hoard. The safety of the cached seeds may depend on whether they are easily pilfered by competitors or lost due to perishability (Hadj-Chikh et al. 1996; Steele et al. 2006; Xiao et al. 2009). Previous studies have found that scatter-hoarding rodents prefer to predate low-tannin seeds but hoard high-tannin seeds as a long-term reserve (Smallwood and Peters 1986; Steele et al. 1996; Xiao et al. 2008). This has been explained by the high tannin content causing the seeds to be less perishable and better suited for storage (Smallwood and Peters 1986). In this study, we suggest an alternative explanation (but the two are not mutually exclusive), that is, that high-tannin seeds were safe because the pilferage risk of high-tannin seeds (e.g. *Q. acutissima*) was consistently lower in all years (Supplementary Figure S1). It is reasonable to think that scatter-hoarding rodents are unlikely to hoard many unsafe seeds, which could be easily stolen by their competitors. The wise choice would be to hoard more safe seeds that could be use after a long period.

We found that cache pilferage risk was not an accurate indicator for determining the probability of scatter-hoarding for different seeds in the high pilferage year (2010). A possible explanation for this may be that scatter-hoarding in high pilferage years is more likely to be a strategy to reduce intense competition under source trees by rapidly sequestering them (Jenkins and Peters 1992; Zhang et al. 2014), but is not a strategy for hoarding seeds for a long period or to keep pilferage at a low level.

Reducing cache pilferage for food-hoarding animals and escaping cache pilferage for plant seeds may be important evolutionary strategies because reducing cache pilferage can help animals get more food, and escaping cache pilferage for plants results in more seeds surviving if they are not consumed by the original hoarders. Seed selection by scatter-hoarding rodents during seed dispersal may be a significant selective pressure on the evolution of seed characteristics related to minimizing cache pilferage. At the same time, the evolution of seed characteristics may significantly affect the evolution of predation and hoarding behaviors of scatter-hoarding animals. In this way, a co-evolutionary arms race may develop. We predicted that the close relationship between seed dispersal by scatter-hoarding rodents and cache pilferage we had found in this study was widespread existed in seed dispersal system of plants and scatter-hoarding animals, including plants-scatter-hoarding rodents and plants-scatter-hoarding birds. Estimation of cache pilferage risk by artificial caches is an efficient method to investigate the effects of cache pilferage on the evolution of predation and hoarding behavior of food-hoarding animals. We recommend future studies on seed dispersal and hoarding behavior of animals to fully consider the effects of cache pilferage by competitors.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online

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