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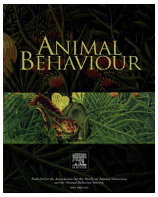

Scatter-hoarding rodents are better pilferers than larder-hoarders

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Food hoarding is critical to rodents for their survival and reproduction. However, the seeds cached by rodents often suffer heavy pilferage by competitors. Therefore, compensation for cache loss is crucial, especially for scatter-hoarding rodents, as they cannot aggressively defend their stored seeds, whereas larder-hoarding rodents can. Pilfering caches of other individuals may be an effective way to compensate for cache loss for rodents. Hence, cache pilfering is likely to be as important as hoarding to food-hoarding rodents. Scatter-hoarding rodents may rely on their olfactory abilities and explore a wide area to retrieve their cached seeds, which may help to increase the probability of encountering and pilfering others' caches, whereas it is not essential for larder-hoarding rodents. We hypothesized that rodents that showed stronger scatter-hoarding behaviour would be better pilferers. To test this hypothesis, we investigated the relationship between scatter-hoarding and pilferage behaviours among four coexisting species of rodents using seminatural enclosure experiments in southwest China. Both hoarding and cache pilfering differed significantly between the four species. The predominant scatter-hoarding rodents, red spiny rats, *Maxomys surifer*, had a strong cache-pilfering behaviour, whereas yellow-bellied rats, *Rattus flavipectus*, mainly adopted larder-hoarding strategies and had a weak cache-pilfering behaviour. Chinese white-bellied rats, *Niviventer confucianus*, and chestnut rats, *Niviventer fulvescens*, had moderate scatter-hoarding and cache-pilfering behaviours. The intensity of cache pilfering was negatively correlated with the intensity of larder hoarding, but positively correlated with the intensity of scatter hoarding among the coexisting food-hoarding rodents. Our study suggests that the positive correlation between the intensities of scatter hoarding and cache pilfering is likely to facilitate reciprocal pilferage among scatter-hoarding rodents, which helps to maintain the stability of scatter-hoarding behaviour in these populations.

Food hoarding is critical to rodents both to survive periods of food shortage and to reproduce (Vander Wall, 1990). Stored food, however, often suffers heavy pilferage due to both interspecific and intraspecific competition (Clarke & Kramer, 1994; Dally, Clayton, & Emery, 2006; Jansen et al., 2012; Lichti, Steele, & Swihart, 2017; Vander Wall et al., 2006). Existing theory of hoarding behaviour predicts that hoarding would not be a stable strategy if the hoarder is not the most likely individual to retrieve the stored foods (Stapanian & Smith, 1978, 1984). However, some studies have found that food-hoarding rodents have evolved a series of strategies to reduce cache pilferage, for example to repeatedly recover and move caches, aggressively defend caches, switch from scatter to larder hoarding (see review by Dally et al., 2006) or directly disperse seeds to areas with low seed density (Geng, Wang, & Cao, 2017; Hirsch, Kays, Pereira, & Jansen, 2012; Munoz & Bonal, 2011) or open areas (Steele et al., 2014, 2015). Relying on these strategies, cache owners can retrieve most of their stored seeds, although many caches are lost by pilfering (Gu, Zhao, & Zhang, 2017). In addition, some rodents appear to compensate for their cache losses by pilfering food reserves of other individuals, which makes pilferage reciprocal among these rodents (Dittel, Perea, & Vander Wall, 2017; Vander Wall & Jenkins, 2003). Therefore, strategies of reducing cache pilferage and reciprocal pilferage among rodents may facilitate the stability of hoarding in rodent populations (Vander Wall & Jenkins, 2003).

Hoarding behaviours usually differ between sympatric rodents, and some species may behave predominantly as scatter-hoarders or as larder-hoarders, whereas others exhibit both scatter and

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larder hoarding (Geng et al., 2017; Hollander & Vander Wall, 2004; Wang, Cao, & Zhang, 2014; Zhang et al., 2016). Larder-hoarding rodents store food items in one or a few sites (e.g. deep underground borrows) and aggressively defend them, which effectively reduces cache pilferage by competitors (Clarke & Kramer, 1994; Dally et al., 2006). In contrast, scatter-hoarding rodents distribute their caches throughout numerous small sites (containing one or a few seeds) across a large area. Therefore, aggressively defending caches appears to be difficult and even impossible for scatter-hoarding rodents. Because high rates of cache pilferage are inevitable, compensation for cache losses is vital to the survival and reproduction of scatter-hoarding rodents. Increasing seed storage or pilfering cached seeds of other rodents will be effective ways to compensate for the losses experienced by scatter-hoarding rodents (Huang, Wang, Zhang, Wu, & Zhang, 2011; Vander Wall & Jenkins, 2003). Increasing seed storage, however, is not always guaranteed, because of the limitations in seed availability due to seasonal fluctuations or mast seeding of seed production (Jansen, Bongers, & Hemerik, 2004; Kelly, 1994; Vander Wall, 2002). Thus, pilfering cached seeds of other rodents seems to be an alternative strategy for scatter-hoarding rodents to compensate for cache losses from pilferers.

The differentiation of hoarding behaviours between sympatric rodents has been well studied (Chang & Zhang, 2014; Hollander & Vander Wall, 2004; Wang et al., 2014; Zhang et al., 2016). In comparison, knowledge about the ability to pilfer caches in sympatric food-hoarding rodents is limited (Vander Wall, Enders, & Waitman, 2009; Yi, Wang, Zhang, & Zhang, 2016) and studies on pilferage behaviour among sympatric food-hoarding rodents at the community level are also rare (but see Dittel et al., 2017). Previous work has shown that the intensity of scatter hoarding (defined as number of seeds scatter-hoarded per rodent individual per unit time) and pilfering (defined as number of seeds pilfered per individual per unit time) may be highly correlated; specifically, cache-pilfering intensity is high in scatter-hoarding rodents (e.g. yellow pine chipmunks, *Tamias amoenus*) and weak in larder-hoarding rodents (e.g. golden-mantled ground squirrels, *Spermophilus lateralis*, Vander Wall et al., 2009). To our knowledge, the relationship between hoarding and pilfering intensities among sympatric food-hoarding rodents at the community level has not been quantitatively investigated. Cache pilfering depends heavily upon the rodents' olfactory ability (Hollander, Vander Wall, & Longland, 2012), and scatter-hoarding rodents could also rely on their olfactory ability to retrieve their own caches (Briggs & Vander Wall, 2004; Steele et al., 2011; Vander Wall, 2000). We thus predicted that the intensity of scatter hoarding and pilfering should be positively correlated.

In this study, we quantitatively investigated the relationship between scatter-hoarding and pilferage behaviours among four sympatric rodent species in seminatural enclosures to test our hypothesis. We predicted that rodents that showed stronger scatter-hoarding behaviour would be better pilferers than those that showed weak scatter-hoarding behaviour, and vice versa.

METHODS

Study Site and Study Species

Our study was conducted in the tropical Xishuangbanna region of Yunnan Province (21°55′N, 101°15′E), southwest China. Tropical montane evergreen broadleaf forest and tropical rainforest are the predominant vegetation types in this region (Zhu, 2006).

Four common rodent species were selected as experimental animals. Red spiny rats, *Maxomys surifer*, and Chinese white-bellied rats, *Niviventer confucianus*, are the dominant rodent species in the tropical montane evergreen broadleaf forests and tropical rainforests (Cao, Guo, & Chen, 2017; Cao et al., 2011; Wang et al., 2014). Chestnut rats, *Niviventer fulvescens*, and yellow-bellied rats, *Rattus flavipectus*, are also common in these forests.

Previous studies have shown that seed traits significantly affect rodent foraging behaviour, including both pilfering and hoarding propensity (Hollander et al., 2012; Zhang et al., 2016). Therefore, we used two species of seeds (*Castanopsis hystrix* and *Pittosporopsis kerrii*) that differed greatly in their traits, to test whether intensity of scatter hoarding was positively correlated with cache pilfering independent of seed species. Both species are the dominant tree species in the tropical montane evergreen broadleaf forest and tropical rainforests, respectively (Lan et al., 2008; Zhu, 2006). The rodents in our study area were frequently observed to eat and hoard seeds of both species (Cao et al., 2016, 2017; Chen, Tomlinson, Cao, & Wang, 2017). The fresh seed mass of *C. hystrix* is 0.93 ± 0.04 g (mean ± SE, $N = 53$), the dry mass is 0.64 ± 0.03 g, the seed coat is thin (0.34 ± 0.01 mm), the tannin content is low (0.15%) and the nutrient content is high (starch 78.7%, fat 0.25% and protein 3.1%; Wang et al., 2014). The fresh seed mass of *P. kerrii* is 5.57 ± 0.14 g ($N = 98$), the dry mass is 2.6 ± 0.2 g, the seed coat thickness is 0.72 ± 0.02 mm, the tannin content is low (0.27%) and the nutrient content is low (starch 38%, fat 1.8% and protein 5.6%; Cao et al., 2011).

Enclosure Experiments

Experiments were conducted in eight seminatural enclosures (10 × 10 m and 1.5 m high; see Wang et al., 2014 for details), which were located within the Xishuangbanna Tropical Botanical Garden (21°54′N, 101°15′E, elevation 550 m).

To avoid the potential influence of repeatedly removing the animals and their cached seeds from enclosures on their subsequent behaviours (Huang et al., 2011), we used different individuals in the hoarding and pilfering experiments (for sample sizes see Table 1). The top of the enclosures was covered with plastic cloth to keep rainwater out. To maintain the same environment during the experiments (Wang et al., 2014), we created wet soil conditions in the enclosures, simulating field conditions, by spraying water evenly for 5 min 1 day before the experiments commenced.

For hoarding experiments, one individual was placed in each enclosure and given laboratory food on the first day, to allow for habituation to the enclosures. On the second day, either 50 marked *C. hystrix* seeds or 40 marked *P. kerrii* were placed at the centre of the enclosure. Seeds were marked by attaching a small coded plastic tag by a thin steel thread (Xiao et al., 2006; Zhang and Wang, 2001). On the third day, we searched the whole enclosure for the seeds. Seed fates were divided into eaten in situ, eaten after being removed, scatter-hoarded (seeds dispersed away from the seed station and buried by rodents under leaf litter or in the soil in a

Table 1
The number of individuals for each rodent species used in hoarding and pilfering experiments for two seed species

Rodent species	No. of individuals	
	Hoarding	Pilfering
Using seeds of *Castanopsis hystrix*		
Maxomys surifer	16	8
Niviventer confucianus	14	8
Niviventer fulvescens	12	8
Rattus flavipectus	16	8
Using seeds of *Pittosporopsis kerrii*		
Maxomys surifer	18	8
Niviventer confucianus	16	8
Niviventer fulvescens	12	8
Rattus flavipectus	11	8

cache of usually one but up to eight seeds) and larder-hoarded (seeds taken into underground burrows).

For pilfering experiments with *C. hystrix* seeds, we first put one individual of *M. surifer* in each of eight enclosures (50 seeds offered per individual), as *M. surifer* is the rodent species showing the most scatter-hoarding behaviour (Cao et al., 2011; Geng et al., 2017). We recorded the scatter-hoarded sites and removed all seeds in each enclosure. Then, we repeatedly buried the same number of seeds in the exact locations where the rodents had established their own caches, which allowed us to set a uniform experimental condition to compare pilfering between rodent species. The numbers of scatter-hoarded sites in the eight enclosures were 10, 10, 13, 14, 20, 24, 42 and 43, respectively. On the first day of the experiment, one marked *C. hystrix* seed was buried under leaf litter at each site where the individuals of *M. surifer* had made their caches. The tag was also buried under leaf litter to eliminate visual cues. On the second day, one rodent individual was introduced into each enclosure and allowed to pilfer the artificial caches. On the third day, we checked the seed fates of the artificial caches. Their fates were divided into pilfered (removed or eaten) or remained, and we searched the enclosure to check the fates of removed seeds. To avoid disturbance from human odour, disposable PVC gloves were worn throughout.

We failed to obtain enough cache sites to perform the pilfering experiments using *P. kerrii* seeds, because rodents scatter-hoarded very few of them. Therefore, we simulated caching behaviour and established 30 caches in three microhabitats (bare ground, under shrubs or near the wall of the enclosure; 10 caches per microhabitat). We detected cache fates of *P. kerrii* seeds using the same method as for *C. hystrix*.

Ethical Note

We captured rodents using live traps made of steel wire mesh (14 × 14 cm and 30 cm high; Chang, Xiao, & Zhang, 2009), baited with shelled peanuts and *P. kerrii* seeds. Carrots were supplied as food and a water source and dry leaves as shelter materials. Traps were checked twice daily in the early morning and late afternoon. Species, body mass, reproductive status and sites of each captured individual were recorded. Pregnant or juvenile individuals were released immediately. Adults of target species were taken back to the laboratory for enclosure experiments. Before the enclosure trials, all rodents were kept in individual cages (40 × 30 cm and 25 cm high) and provided with nest material, commercial mouse chow (provided by Animal Experiment Center of Sichuan University, Chengdu, China), apple, corn and water ad libitum. A photoperiod cycle of 12:12 h (light:dark) was maintained. All the animals were held in captivity for less than 20 days. After the experiments, all animals were examined by a veterinarian to ensure their health prior to release at the original sites of capture. Returning animals to the location where they were trapped is not the same as putting them back into the environment from which they were taken because trapping some individuals might change the social conditions. However, these rodents disperse frequently and might easily adapt to conditions at the release site.

This study followed the Guidelines for the care and use of laboratory animals of China and the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching, and was approved by the Institute of Zoology, and Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

Data Analysis

Generalized linear models (GLMs) were used to analyse differences in the proportion of larder hoarding, scatter hoarding and cache pilfering between the four rodent species, using R version 3.4.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org), while rodent species was treated as a fixed variable. The sampling unit was the proportion of seeds larder-hoarded, scatter-hoarded (the proportion of the seeds presented to each individual; sample sizes and fates of seeds for each individual are given in Appendix Tables A1 and A2) or pilfered (proportion of the presented seeds; Appendix Table A3) by an individual, modelled as a binomial distribution with a logit-link function. Tukey's test (implemented through the lsmeans package) was applied for post hoc pairwise comparison between rodent species. Analysis of variance with Wald chi-square tests were performed to test the significance of fixed categorical variables in GLMs using the Anova function in the car package of R software. Because no seeds of *C. hystrix* were scatter-hoarded by *R. flavipectus*, this rodent species was excluded when we analysed the differences in the proportion of scatter hoarding between species.

We used the Pearson chi-square test and Fisher's exact test (using SPSS for Windows 20.0) to compare the fates of pilfered seeds (larder-hoarded and scatter-hoarded) between rodent species. We only did this analysis at the species scale, not at the individual scale, because of the small sample size of seeds pilfered by each individual, especially for *N. fulvescens* and *R. flavipectus* (Appendix Table A3).

RESULTS

Hoarding Behaviour

The proportions of larder-hoarded (*C. hystrix*: $\chi^2_3 = 510.8$, $P < 0.0001$; Fig. 1a; *P. kerrii*: $\chi^2_3 = 310$, $P < 0.0001$; Fig. 1d, Table 2) and scatter-hoarded seeds (*C. hystrix*: $\chi^2_2 = 218.1$, $P < 0.0001$; Fig. 1b; *P. kerrii*: $\chi^2_3 = 266.9$, $P < 0.0001$; Fig. 1e, Table 2) for both plant species differed significantly between the four species of rodents. The proportions of larder hoarding for both seed species were highest for *R. flavipectus*, followed by *N. confucianus*, *N. fulvescens* and *M. surifer*. The proportions of scatter hoarding for both seed species were highest for *M. surifer*, followed by *N. confucianus*, *N. fulvescens* and *R. flavipectus*.

Pilfering Behaviour

The pilfering intensity differed significantly between the four species of rodents provided with the two seed species (*C. hystrix*: $\chi^2_3 = 86.6$, $P = 0.001$; Fig. 1c; *P. kerrii*: $\chi^2_3 = 50.5$, $P < 0.0001$; Fig. 1f, Table 2). The proportion of cache pilfering for both seed species was highest for *M. surifer*, followed by *N. confucianus*, *N. fulvescens* and *R. flavipectus*.

Of the pilfered seeds, *R. flavipectus* larder-hoarded more of them than the other three species (Fig. 2a, c; results of Pearson chi-square and Fisher's exact tests are shown in Appendix Table A5), similar to the results of the hoarding experiments. More pilfered seeds were scatter-hoarded by *M. surifer* and *N. confucianus* than by *R. flavipectus* and *N. fulvescens* (Fig. 2b, d).

Relationship Between Hoarding and Cache Pilfering

For both seed species, *M. surifer* showed the highest, and *R. flavipectus* the lowest, proportion of both scatter hoarding and cache pilfering. Both *N. confucianus* and *N. fulvescens* showed moderate proportions of scatter hoarding and cache pilfering for both seed species. These results indicate that the proportion of cache pilfering was positively correlated with that of scatter hoarding, but negatively correlated with the proportion of larder hoarding between rodent species.

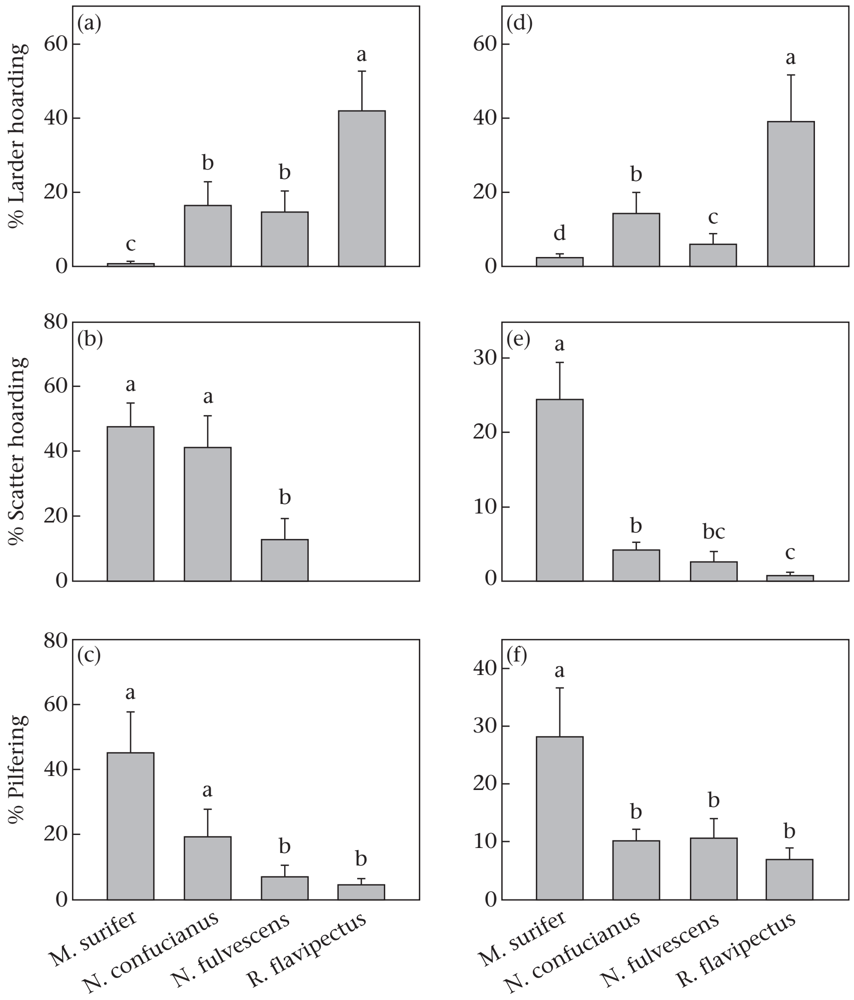

Figure 1. The differences in the percentages (means + SE) of (a, d) larder hoarding, (b, e) scatter hoarding (in hoarding experiments) and (c, f) pilfering (in pilfering experiments) between rodent species for (a, b, c) *C. hystrix* seeds and (d, e, f) *P. kerrii* seeds. Different letters indicate significant differences between species ($P < 0.05$, a > b > c > d). The number of seeds presented was 50 (a, b; *C. hystrix*) or 40 (d, e; *P. kerrii*) for each individual in the hoarding experiments and 10–43 (c; *C. hystrix*) or 30 (f; *P. kerrii*) for each individual in the pilfering experiments. Sample sizes and seed fates for each individual are shown in Appendix Tables A1–A3.

In addition, *N. confucianus* scatter-hoarded a larger proportion of, and showed a stronger cache-pilfering intensity for, *C. hysrix* seeds, compared with *P. kerrii* seeds (scatter hoarding: $\chi^2_1 = 291.7$, $P < 0.0001$; pilfering: $\chi^2_1 = 17.6$, $P < 0.0001$).

DISCUSSION

Our results indicated that both hoarding and the intensity of cache pilfering differed significantly between four coexisting food-hoarding rodents. *Maxomys surifer* predominantly scatter-hoarded both seed species, *R. flavipectus* predominantly larder-hoarded and *N. confucianus* and *N. fulvescens* did both. Cache-pilfering intensity was strong in *M. surifer* for both seed species, weak in *R. flavipectus* and moderate in *N. confucianus* and *N. fulvescens*. These results indicated that cache-pilfering intensity was positively correlated with scatter hoarding, but negatively correlated with larder hoarding. This correlation is likely to facilitate reciprocal pilferage among scatter-hoarding rodents and maintain the stability of scatter hoarding in the population (Dittel et al., 2017; Vander Wall & Jenkins, 2003).

Strong cache-pilfering intensity is important to scatter-hoarding rodents: pilfering food reserves of other rodents helps to compensate for cache losses, which is critical to survival and reproduction for scatter-hoarding rodents. Previous studies suggested that pilferage was reciprocal among coexisting food-hoarding rodents (Dittel et al., 2017; Vander Wall & Jenkins, 2003). However, if pure thieves, for example larder-hoarding *R. flavipectus* in this study, pilfer many seeds cached by scatter-hoarding rodents that cannot reciprocate, the pilfered seeds will be consumed or larder-hoarded after pilfering, but not scatter-hoarded elsewhere, similar to our results (see Fig. 2). There will thus be no seeds available for the original hoarders to pilfer, and the pilferage will no longer be reciprocal; therefore, scatter hoarding would not be a stable strategy in the population (Stapanian & Smith, 1978, 1984). To achieve symmetrical pilferage and maintain the stability of hoarding, a positive correlation between the intensities of scatter hoarding and cache pilfering is necessary among the coexisting food-hoarding rodents. Thus, it is likely that scatter hoarding and cache pilfering evolved together, not separately, during the evolutionary history of foraging behaviours in food-hoarding rodents. A strong scatter-hoarding behaviour is expected to be accompanied by a strong cache-pilfering intensity in food-hoarding rodents, and vice versa. Our results concur with previous work that showed that a scatter-hoarding rodent, the yellow pine chipmunk, had a strong cache-pilfering intensity, while a larder-hoarding rodent, a ground squirrel, had a weak one (Vander Wall et al., 2009). Moreover, Dittel et al. (2017) found that the number of caches

Table 2
The summary of GLMs analysing the differences in larder hoarding, scatter hoarding and cache pilfering between the four rodents

	Estimate ± SE	*z*	*P*
Larder hoarding (using *C. hystrix* seeds)			
(Intercept)	−4.73 ± 0.38	−12.5	<0.0001
N. confucianus	3.11 ± 0.39	7.9	<0.0001
N. fulvescens	2.97 ± 0.4	7.5	<0.0001
R. flavipectus	4.41 ± 0.39	11.4	<0.0001
Larder hoarding (using *P. kerrii* seeds)			
(Intercept)	−3.61 ± 0.23	−15.52	<0.0001
N. confucianus	1.84 ± 0.26	7.11	<0.0001
N. fulvescens	0.86 ± 0.3	2.87	0.004
R. flavipectus	3.16 ± 0.25	12.55	<0.0001
Scatter hoarding (using *C. hystrix* seeds)[a]			
(Intercept)	−0.12 ± 0.07	−1.6	0.104
N. confucianus	−0.25 ± 0.1	−2.4	0.017
N. fulvescens	−1.83 ± 0.14	−12.9	<0.0001
Scatter hoarding (using *P. kerrii* seeds)			
(Intercept)	−1.13 ± 0.09	−13.0	<0.0001
N. confucianus	−2.03 ± 0.22	−9.3	<0.0001
N. fulvescens	−2.54 ± 0.3	−8.3	<0.0001
R. flavipectus	−3.85 ± 0.59	−6.6	<0.0001
Cache pilfering (using *C. hystrix* seeds)			
(Intercept)	−0.71 ± 0.16	−4.4	<0.0001
N. confucianus	−0.36 ± 0.24	−1.5	0.129
N. fulvescens	−2.21 ± 0.38	−5.8	<0.0001
R. flavipectus	−2.47 ± 0.42	−5.9	<0.0001
Cache pilfering (using *P. kerrii* seeds)			
(Intercept)	−0.95 ± 0.14	−6.6	<0.0001
N. confucianus	−1.25 ± 0.26	−4.8	<0.0001
N. fulvescens	−1.2 ± 0.26	−4.7	<0.0001
R. flavipectus	−1.69 ± 0.3	−5.7	<0.0001

The results in this table show comparisons between *M. surifer* and the other three rodent species (*N. confucianus*, *N. fulvescens*, *R. flavipectus*).

[a] As *R. flavipectus* did not scatter-hoard any *C. hystrix* seeds, it was excluded from the analysis of the differences in the proportion of scatter hoarding between rodent species.

lost and gained by pilfering was almost the same among three species of sympatric scatter-hoarding rodents, but the number of caches lost was greater than the number gained among species exhibiting larder hoarding.

Why do rodents that predominantly scatter-hoard show a strong cache-pilfering intensity? Possible reasons could be food exploration patterns and olfactory abilities of scatter-hoarding rodents. It is well established that scatter-hoarders rely not only on spatial memory (Hirsch, Kays, & Jansen, 2013; Huston & Oitzl, 1989; Smulders, Gould, & Leaver, 2010), but also on their strong olfactory abilities to retrieve their own caches (Briggs & Vander Wall, 2004; Steele et al., 2011; Vander Wall, 2000). It has been proposed that scatter-hoarding rodents locate their cache initially using spatial memory, and secondarily use their olfactory abilities to retrieve the seeds. Strong olfactory ability not only helps them to relocate their own caches, but also may increase their ability to pilfer cached seeds of other rodents. In addition, scatter-hoarding rodents need to explore a wide area to collect or retrieve their cached seeds, because they often spread their caches across a large area (Vander Wall, 1990, 2001). Thus, they are more likely to encounter caches belonging to other rodents.

In our study, the larder-hoarding rodents exhibited a weak cache-pilfering intensity. The possible reason for this observation is that cache pilfering is not as important for larder-hoarding rodents as for scatter-hoarding rodents. Larder-hoarding rodents usually hoard all their seeds in one or a few sites, such as tree holes or their underground burrows. They aggressively defend their caches to prevent cache pilferage by competitors (Dally et al., 2006). Indeed, the larder-hoarding species *R. flavipectus* was more aggressive than the other three species (Z. Wang and L. Cao, personal observation). Previous studies found that larder-hoarding animals aggressively defend their caches by excluding potential competitors from their territory or area around their burrow (Clarke & Kramer, 1994a; Jenkins & Breck, 1998; Price, 1994). Strong olfactory abilities and intensive search effort, which may increase the probability of encountering and pilfering others' caches, may not be essential for larder-hoarding rodents to retrieve or defend their caches; thus, they have a low ability to pilfer cached seeds of other rodents. It would be interesting to study the relationships between aggressiveness and hoarding of coexisting food-hoarding animals (e.g. rodents and birds) and between the food exploration patterns (or

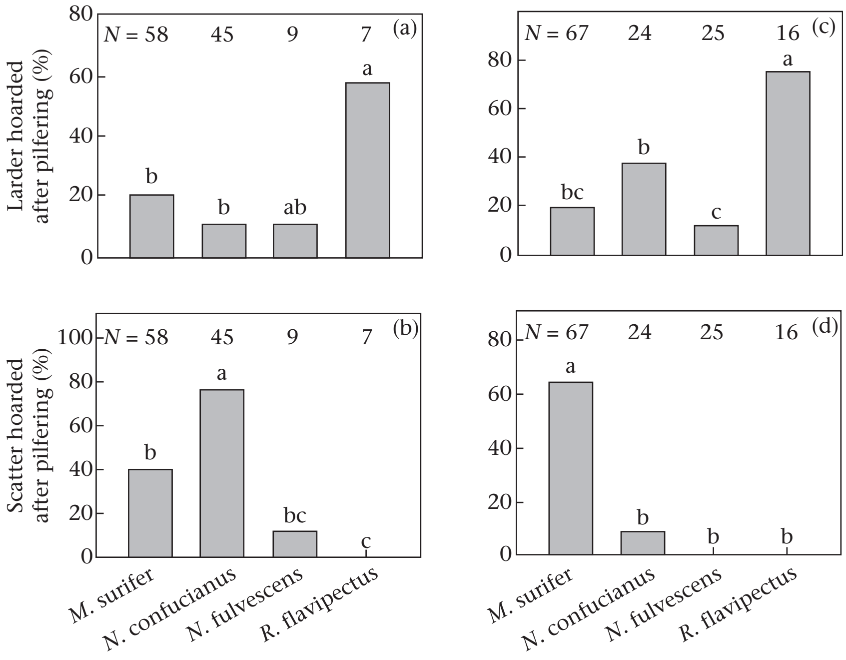

Figure 2. The differences in the percentages of (a, c) larder hoarding and (b, d) scatter hoarding of pilfered seeds between four rodent species for (a, b) *C. hystrix* seeds and (c, d) *P. kerrii* seeds. Different letters indicate significant differences between species ($P < 0.05$, a > b > c > d). *N* is the total number of seeds pilfered by all individuals within a species. Sample sizes and seed fates for each individual are shown in Appendix Table A4.

searching efforts) and pilferage intensity of these animals. It will help us further understand the evolution of hoarding and pilfering in food-hoarding animals.

Our results also showed that the intensities of hoarding and pilfering were seed-species dependent. *Niviventer confucianus* scatter-hoarded a large percentage of *C. hystrix* seeds (41%), but few *P. kerrii* seeds (4.1%). Previous studies also found that hoarding differed when different species of seeds were encountered by a given rodent (Chang & Zhang, 2014; Wang et al., 2014; Zhang et al., 2016). Similarly, *N. confucianus* pilfered a high percentage of *C. hystrix* seeds (19.3%), but few *P. kerrii* seeds (10%). These differences can be attributed to different preferences of rodents for seeds with contrasting traits (Wang et al., 2014). The intensity of scatter hoarding and pilfering in *N. confucianus* decreased (or increased) simultaneously when encountering different seeds, which further supports our conclusion that scatter-hoarding and cache-pilfering intensities are well matched in food-hoarding rodents. We expected food-hoarding rodents to display different caching and pilfering intensities when encountering seeds with different traits; however, the relationship between the scatter-hoarding and cache-pilfering intensities of rodents was positive despite differences in seed species. Our results suggest that different sources of seeds could affect hoarding by rodents. For example, *M. surifer* larder-hoarded less than 2% of seeds in the hoarding experiments (Fig. 1a and b), but larder-hoarded nearly 20% of the seeds pilfered from artificial caches in pilfering experiments (Fig. 2a and b). Our results may help us understand the switching mechanism between scatter and larder hoarding in food-hoarding animals (Clarke & Kramer, 1994; Dally et al., 2006; Vander Wall, Hager, & Kuhn, 2005).

As cache pilfering and hoarding are common in many animal species (Dally et al., 2006; Vander Wall & Jenkins, 2003), we expect the mechanism observed here could also be useful to explain the food-hoarding behaviour of other hoarding animals, such as corvids. However, birds may show different mechanisms from rodents, when they retrieve their own caches or pilfer caches of other animals. For example, birds may not rely on olfaction to search for stored seeds, but they may directly observe other individuals storing seeds and use observational spatial memory to pilfer others' caches (Daily, Emery, & Clayton, 2004, 2005).

In this study, we investigated the differentiation in the intensities of cache pilfering between different rodent species under well-controlled experimental conditions. Therefore, the observed differences can be mainly attributed to differences in the intrinsic characteristics or behaviours between species. However, many other factors may affect cache pilferage in the field, such as seed species, seed abundance, density of rodents, risks of predation, cache density and soil water content (Cao et al., 2018; Galvez, Kranstauber, Kays, & Jansen, 2009; Lichti et al., 2017; Vander Wall, 2000). In this study, we only investigated the relationships between hoarding and pilfering at the interspecific level; however, we found that they also differed between individuals within species. We suggest future studies should combine the effects of some other potential factors and test the interactions between hoarding and pilfering at both the species and the individual level.

In conclusion, our study indicates that hoarding and cache-pilfering intensity differ significantly between coexisting food-hoarding rodents. Scatter-hoarding intensity was positively correlated with cache-pilfering intensity, indicating that scatter hoarding and cache pilfering may evolve together in food-hoarding rodents. Concurrent evolution of strong cache pilfering and scatter hoarding is essential to scatter-hoarding rodents, enabling reciprocal pilferage among coexisting food-hoarding rodents and stabilizing scatter hoarding in the population.

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References

Briggs, J. S., & Vander Wall, S. B. (2004). Substrate type affects caching and pilferage of pine seeds by chipmunks. *Behavioral Ecology, 15*(4), 666–672.

Cao, L., Guo, C., & Chen, J. (2017). Fluctuation in seed abundance has contrasting effects on the fate of seeds from two rapidly geminating tree species in an Asian tropical forest. *Integrative Zoology, 12*, 2–11.

Cao, L., Wang, Z. Y., Yan, C., Chen, J., Guo, C., & Zhang, Z. B. (2016). Differential foraging preferences on seed size by rodents result in higher dispersal success of medium-sized seeds. *Ecology, 97*(11), 3070–3078.

Cao, L., Wang, B., Yan, C., Wang, Z. Y., Zhang, H. M., Geng, Y. Z., et al. (2018). Risk of cache pilferage determines hoarding behavior of rodents and seed fate. *Behavioral Ecology*. https://doi.org/10.1093/beheco/ary040. In press.

Cao, L., Xiao, Z. S., Wang, Z. Y., Guo, C., Chen, J., & Zhang, Z. B. (2011). High regeneration capacity helps tropical seeds to counter rodent predation. *Oecologia, 166*, 997–1007.

Chang, G., Xiao, Z. S., & Zhang, Z. B. (2009). Hoarding decisions by Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*): The responses to seed size and germination schedule in acorns. *Behavioural Processes, 82*(1), 7–11.

Chang, G., & Zhang, Z. B. (2014). Functional traits determine formation of mutualism and predation interactions in seed-rodent dispersal system of a subtropical forest. *Acta Oecologica, 55*, 43–50.

Chen, Q., Tomlinson, K. W., Cao, L., & Wang, B. (2017). Effects of fragmentation on the seed predation and dispersal by rodents differ among species with different seed size. *Integrative Zoology, 12*, 468–476.

Clarke, M. F., & Kramer, D. L. (1994a). The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. *Behavioral Ecology, 5*(4), 353–361.

Clarke, M. F., & Kramer, D. L. (1994b). Scatter-hoarding by a larder-hoarding rodent: Intraspecific variation in the hoarding behavior of the eastern chipmunk, *Tamias striatus*. *Animal Behaviour, 48*(2), 299–308.

Daily, J. M., Emery, N. J., & Clayton, N. S. (2004). Cache protection strategies by western scrub-jays (*Aphelocoma californica*): Hiding food in the shade. *Proceedings of the Royal Society B: Biological Sciences, 271*, S387–S390.

Dally, J. M., Clayton, N. S., & Emery, N. J. (2006). The behaviour and evolution of cache protection and pilferage. *Animal Behaviour, 72*, 13–23.

Dally, J. M., Emery, N. J., & Clayton, N. S. (2005). Cache protection strategies by western scrub-jays *Aphelocoma californica*: Implications for social cognition. *Animal Behaviour, 70*, 1251–1263.

Dittel, J. W., Perea, R., & Vander Wall, S. B. (2017). Reciprocal pilfering in a seed-caching rodent community: Implications for species coexistence. *Behavioral Ecology and Sociobiology, 71*(10).

Galvez, D., Kranstauber, B., Kays, R. W., & Jansen, P. A. (2009). Scatter hoarding by the Central American agouti: A test of optimal cache spacing theory. *Animal Behaviour, 78*(6), 1327–1333.

Geng, Y. Z., Wang, B., & Cao, L. (2017). Directed seed dispersal by scatter-hoarding rodents into areas with a low density of conspecific seeds in the absence of pilferage. *Journal of Mammalogy, 98*(6), 1682–1687.

Gu, H. F., Zhao, Q. J., & Zhang, Z. B. (2017). Does scatter-hoarding of seeds benefit cache owners or pilferers? *Integrative Zoology, 12*(6), 477–488.

Hirsch, B. T., Kays, R., & Jansen, P. A. (2013). Evidence for cache surveillance by a scatter-hoarding rodent. *Animal Behaviour, 85*(6), 1511–1516.

Hirsch, B. T., Kays, R., Pereira, V. E., & Jansen, P. A. (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters, 15*, 1423–1429.

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

Hollander, J. L., Vander Wall, S. B., & Longland, W. S. (2012). Olfactory detection of caches containing wildland versus cultivated seeds by granivorous rodents. *Western North American Naturalist, 72*(3), 339–347.

Huang, Z. Y., Wang, Y., Zhang, H. M., Wu, F. Q., & Zhang, Z. B. (2011). Behavioural responses of sympatric rodents to complete pilferage. *Animal Behaviour, 81*, 831–836.

Huston, J. P., & Oitzl, M. S. (1989). The relationship between reinforcement and memory parallels in the rewarding and mnemonic effects of the neuropeptide substance-P. *Neuroscience & Biobehavioral Reviews, 13*(2–3), 171–180.

Jansen, P. A., Bongers, F., & Hemerik, L. (2004). Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs, 74*(4), 569–589.

Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America, 109*(31), 12610–12615.

Jenkins, S. H., & Breck, S. W. (1998). Differences in food hoarding among six species of heteromyid rodents. *Journal of Mammalogy, 79*(4), 1221–1233.

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution, 9*(12), 465–470.

Lan, G. Y., Hu, Y. H., Cao, M., Zhu, H., Wang, H., & Zhou, S. S. (2008). Establishment of Xishuangbanna tropical forest dynamics plot: Species compositions and spatial distribution patterns. *Journal of Plant Ecology Sinica, 32*, 287–298.

Lichti, N. I., Steele, M. A., & Swihart, R. K. (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews, 92*(1), 474–504.

Munoz, A., & Bonal, R. (2011). Linking seed dispersal to cache protection strategies. *Journal of Ecology, 99*(4), 1016–1025.

Price, K. (1994). Center edge effect in red squirrels: Evidence from playback experiments. *Journal of Mammalogy, 75*(2), 545–548.

Smulders, T. V., Gould, K. L., & Leaver, L. A. (2010). Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1542), 883–900.

Stapanian, M. A., & Smith, C. C. (1978). A model of seed scatter hoarding: Coevolution of fox squirrels and black walnuts. *Ecology, 59*, 884–896.

Stapanian, M. A., & Smith, C. C. (1984). Density dependent survival of scatter-hoarded nuts: An experimental approach. *Ecology, 65*(5), 1387–1396.

Steele, M. A., Bugdal, M., Yuan, A., Bartlow, A., Buzalewski, J., Lichti, N., et al. (2011). Cache placement, pilfering, and a recovery advantage in a seed-dispersing rodent: Could predation of scatter hoarders contribute to seedling establishment? *Acta Oecologica, 37*(6), 554–560.

Steele, M. A., Contreras, T. A., Hadj-Chikh, L. Z., Agosta, S. J., Smallwood, P. D., & Tomlinson, C. N. (2014). Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behavioral Ecology, 25*(1), 206–215.

Steele, M. A., Rompre, G., Stratford, J. A., Zhang, H. M., Suchocki, M., & Marino, S. (2015). Scatterhoarding rodents favor higher predation risks for cache sites: The potential for predators to influence the seed dispersal process. *Integrative Zoology, 10*(3), 257–266.

Vander Wall, S. B. (1990). *Food hoarding in animals*. Chicago, IL: University of Chicago Press.

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

Vander Wall, S. B. (2001). The evolutionary ecology of nut dispersal. *The Botanical Review, 67*(1), 74–117.

Vander Wall, S. B. (2002). Masting in animal-dispersed pines facilitates seed dispersal. *Ecology, 83*(12), 3508–3516.

Vander Wall, S. B., Briggs, J. S., Jenkins, S. H., Kuhn, K. M., Thayer, T. C., & Beck, M. J. (2006). Do food-hoarding animals have a cache recovery advantage? Determining recovery of stored food. *Animal Behaviour, 72*, 189–197.

Vander Wall, S. B., Enders, M. S., & Waitman, B. A. (2009). Asymmetrical cache pilfering between yellow pine chipmunks and golden-mantled ground squirrels. *Animal Behaviour, 78*(2), 555–561.

Vander Wall, S. B., Hager, E. C. H., & Kuhn, K. M. (2005). Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. *Western North American Naturalist, 65*(2), 248–257.

Vander Wall, S. B., & Jenkins, S. H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology, 14*(5), 656–667.

Wang, Z. Y., Cao, L., & Zhang, Z. B. (2014). Seed traits and taxonomic relationships determine the occurrence of mutualisms versus seed predation in a tropical forest rodent and seed dispersal system. *Integrative Zoology, 9*, 309–319.

Xiao, Z. S., Jansen, P. A., & Zhang, Z. B. (2006). Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management, 223*, 18–23.

Yi, X. F., Wang, Z. Y., Zhang, H. M., & Zhang, Z. B. (2016). Weak olfaction increases seed scatter-hoarding by Siberian chipmunks: Implication in shaping plant. *Oikos, 125*(12), 1712–1718.

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

Zhang, Z. B., Wang, Z. Y., Chang, G., Yi, X. F., Lu, J. Q., Xiao, Z. S., et al. (2016). Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. *Plant Ecology, 217*(3), 253–265.

Zhu, H. (2006). Forest vegetation of Xishuangbanna, south China. *Forestry Studies in China, 8*(2), 1–58.

APPENDIX

Table A1

The number of seeds larder-hoarded or scatter-hoarded by each individual for four rodent species in hoarding experiments when using *Castanopsis hystrix* seeds

Maxomys surifer				*Niviventer confucianus*				*Niviventer fulvescens*				*Rattus flavipectus*			
Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total
Sur1	1	27	50	Con1	1	0	50	Ful1	10	0	50	Fla1	2	0	50
Sur2	0	15	50	Con2	7	0	50	Ful2	11	0	50	Fla2	50	0	50
Sur3	0	6	50	Con3	45	0	50	Ful3	1	0	50	Fla3	47	0	50
Sur4	1	41	50	Con4	12	37	50	Ful4	3	42	50	Fla4	4	0	50
Sur5	1	32	50	Con5	1	6	50	Ful5	10	4	50	Fla5	24	0	50
Sur6	0	30	50	Con6	4	44	50	Ful6	5	0	50	Fla6	6	0	50
Sur7	0	37	50	Con7	1	17	50	Ful7	0	6	50	Fla7	50	0	50
Sur8	0	32	50	Con8	1	40	50	Ful8	12	11	50	Fla8	6	0	50
Sur9	0	2	50	Con9	0	12	50	Ful9	35	6	50	Fla9	1	0	50
Sur10	0	33	50	Con10	9	37	50	Ful10	1	0	50	Fla10	31	0	50
Sur11	0	29	50	Con11	7	42	50	Ful11	0	4	50	Fla11	1	0	50
Sur12	0	44	50	Con12	6	40	50	Ful12	0	2	50	Fla12	49	0	50
Sur13	4	37	50	Con13	18	2	50	–	–	–	50	Fla13	0	0	50
Sur14	0	4	50	Con14	4	10	50	–	–	–	50	Fla14	50	0	50
Sur15	0	7	50	–	–	–	–	–	–	–	50	Fla15	13	0	50
Sur16	0	1	50	–	–	–	–	–	–	–	50	Fla16	2	0	50
Mean	0.4 ± 1.0	23.6 ± 15.1	50	Mean	8.3 ± 11.7	20.8 ± 18.2	50	Mean	7.3 ± 9.9	6.3 ± 11.8	50	Mean	21 ± 21.4	0	50

Total: the total sample of seeds presented to an individual. Mean: the mean number (±SD) of seeds larder-hoarded or scatter-hoarded by an individual in a species.

Table A2
The number of seeds larder-hoarded or scatter-hoarded by each rodent individual for four rodent species in hoarding experiments when using *Pittosporopsis kerrii* seeds

Maxomys surifer				*Niviventer confucianus*				*Niviventer fulvescens*				*Rattus flavipectus*			
Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total
Sur17	0	3	40	Con15	1	1	40	Ful13	2	0	40	Fla17	0	0	40
Sur18	1	3	40	Con16	7	1	40	Ful14	2	0	40	Fla18	1	0	40
Sur19	0	8	40	Con17	3	0	40	Ful15	0	1	40	Fla19	2	1	40
Sur20	0	10	40	Con18	8	0	40	Ful16	10	7	40	Fla20	40	0	40
Sur21	0	5	40	Con19	0	3	40	Ful17	0	4	40	Fla21	11	0	40
Sur22	0	7	40	Con20	3	1	40	Ful18	12	0	40	Fla22	13	2	40
Sur23	3	5	40	Con21	1	1	40	Ful19	1	0	40	Fla23	40	0	40
Sur24	0	0	40	Con22	33	1	40	Ful20	1	0	40	Fla24	2	0	40
Sur25	4	8	40	Con23	2	6	40	Ful21	1	0	40	Fla25	23	0	40
Sur26	0	8	40	Con24	10	0	40	Ful22	0	0	40	Fla26	2	0	40
Sur27	0	18	40	Con25	2	4	40	Ful23	0	0	40	Fla27	38	0	40
Sur28	2	8	40	Con26	17	1	40	Ful24	0	0	40	–	–	–	–
Sur29	1	22	40	Con27	3	1	40	–	–	–	–	–	–	–	–
Sur30	0	10	40	Con28	0	2	40	–	–	–	–	–	–	–	–
Sur31	3	6	40	Con29	0	1	40	–	–	–	–	–	–	–	–
Sur32	2	4	40	Con30	3	3	40	–	–	–	–	–	–	–	–
Sur33	3	36	40	–	–	–	–	–	–	–	–	–	–	–	–
Sur34	0	15	40	–	–	–	–	–	–	–	–	–	–	–	–
Mean	1.1 ± 1.4	9.8 ± 8.5	40	Mean	5.8 ± 8.4	1.6 ± 1.6	40	Mean	2.4 ± 4.1	1 ± 2.2	40	Mean	15.6 ± 16.7	0.3 ± 0.6	40

Total: the total sample of seeds presented to an individual. Mean: the mean number (±SD) of seeds larder-hoarded or scatter-hoarded by an individual in a species.

Table A3
The number of seeds pilfered by each individual for four rodent species in pilfering experiments

Maxomys surifer			*Niviventer confucianus*			*Niviventer fulvescens*			*Rattus flavipectus*		
Individual	Pilfered	Total sample	Individual	Pilfered	Total sample	Individual	Pilfered	Total sample	Individual	Pilfered	Total sample
Using *Castanopsis hystrix* seeds											
Sur35	4	10	Con31	0	10	Ful25	2	10	Fla28	1	10
Sur36	2	10	Con32	2	10	Ful26	0	10	Fla29	0	10
Sur37	12	13	Con33	1	13	Ful27	1	13	Fla30	0	13
Sur38	14	14	Con34	0	14	Ful28	0	14	Fla31	1	14
Sur39	11	20	Con35	2	20	Ful29	5	20	Fla32	3	20
Sur40	10	24	Con36	12	24	Ful30	0	24	Fla33	0	24
Sur41	2	42	Con37	27	42	Ful31	1	42	Fla34	0	42
Sur42	3	43	Con38	1	43	Ful32	0	43	Fla35	2	43
Mean	7.3 ± 5.0	22 ± 13.5	Mean	5.6 ± 9.5	22 ± 13.5	Mean	1.1 ± 1.7	22 ± 13.5	Mean	0.9 ± 1.1	22 ± 13.5
Using *Pittosporopsis kerrii* seeds											
Sur43	3	30	Con39	2	30	Ful33	1	30	Fla36	2	30
Sur44	22	30	Con40	7	30	Ful34	0	30	Fla37	0	30
Sur45	16	30	Con41	4	30	Ful35	9	30	Fla38	1	30
Sur46	11	30	Con42	2	30	Ful36	2	30	Fla39	0	30
Sur47	3	30	Con43	1	30	Ful37	2	30	Fla40	3	30
Sur48	1	30	Con44	2	30	Ful38	5	30	Fla41	1	30
Sur49	4	30	Con45	2	30	Ful39	0	30	Fla42	4	30
Sur50	7	30	Con46	4	30	Ful40	6	30	Fla43	5	30
Mean	8.4 ± 7.4	30	Mean	3 ± 1.9	30	Mean	3.1 ± 3.2	30	Mean	2 ± 1.9	30

Total sample: the total sample of seeds presented to an individual. Mean: the mean number (±SD) of seeds pilfered by an individual in a species.

Table A4
The number of pilfered seeds larder-hoarded or scatter-hoarded by each rodent individual in pilfering experiments

Maxomys surifer				*Niviventer confucianus*				*Niviventer fulvescens*				*Rattus flavipectus*			
Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total	Individual	Larder hoarded	Scatter hoarded	Total
Using *Castanopsis hystrix* seeds															
Sur35	2	1	4	Con31	0	0	0	Ful25	0	0	2	Fla28	0	0	1
Sur36	1	1	2	Con32	0	1	2	Ful26	0	0	0	Fla29	0	0	0
Sur37	8	4	12	Con33	0	1	1	Ful27	1	0	1	Fla30	0	0	0
Sur38	0	6	14	Con34	0	0	0	Ful28	0	0	0	Fla31	0	0	1
Sur39	0	2	11	Con35	0	0	2	Ful29	0	1	5	Fla32	3	0	3
Sur40	0	8	10	Con36	0	10	12	Ful30	0	0	0	Fla33	0	0	0
Sur41	1	1	2	Con37	5	21	27	Ful31	0	0	1	Fla34	0	0	0
Sur42	0	0	3	Con38	0	1	1	Ful32	0	0	0	Fla35	1	0	2
Mean	1.5 ± 2.7	2.9 ± 2.9	7.3 ± 5.0	Mean	0.6 ± 1.8	4.3 ± 7.6	5.6 ± 9.5	Mean	0.1 ± 0.4	0.1 ± 0.4	1.1 ± 1.7	Mean	0.5 ± 1.1	0	0.9 ± 1.1
Using *Pittosporopsis kerrii* seeds															
Sur43	2	1	3	Con39	0	0	2	Ful33	1	0	1	Fla36	2	0	2
Sur44	2	20	22	Con40	5	0	7	Ful34	0	0	0	Fla37	0	0	0
Sur45	5	10	16	Con41	2	1	4	Ful35	1	0	9	Fla38	1	0	1
Sur46	0	4	11	Con42	1	0	2	Ful36	1	0	2	Fla39	0	0	0
Sur47	2	1	3	Con43	0	0	1	Ful37	0	0	2	Fla40	3	0	3
Sur48	1	0	1	Con44	1	1	2	Ful38	0	0	5	Fla41	1	0	1
Sur49	0	1	4	Con45	0	0	2	Ful39	0	0	0	Fla42	3	0	4
Sur50	1	6	7	Con46	0	0	4	Ful40	0	0	6	Fla43	2	0	5
Mean	1.6 ± 1.6	5.4 ± 6.8	8.4 ± 7.4	Mean	1.1 ± 1.7	0.3 ± 0.5	3 ± 1.9	Mean	0.4 ± 0.5	0	3.1 ± 3.2	Mean	1.5 ± 1.2	0	2 ± 1.9

Total: the total number of seeds pilfered by an individual. Mean: the mean number (±SD) of seeds larder-hoarded or scatter-hoarded by an individual after pilferage in a species.

Table A5
Comparison of the fates of pilfered seeds between rodent species

Pairwise between species	Using *Castanopsis hystrix* seeds				Using *Pittosporopsis kerrii* seeds			
	Larder hoarding		Scatter hoarding		Larder hoarding		Scatter hoarding	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
M. surifer and *N. confucianus*	1.7	0.194	13.2	<0.001	3.2	0.076	–*	<0.001
M. surifer and *N. fulvescens*	–*	0.677	–*	0.142	0.7	0.405	–*	<0.001
M. surifer and *R. flavipectus*	4.5	0.034	–*	0.045	19.0	<0.001	–*	<0.001
N. confucianus and *N. fulvescens*	–*	1	–*	0.001	4.3	0.038	–*	0.235
N. confucianus and *R. flavipectus*	9.0	0.003	–*	<0.001	5.4	0.02	–*	0.508
N. fulvescens and *R. flavipectus*	–*	0.106	–*	1	16.7	<0.001	–	–

Comparisons were done with the Pearson chi-square test, except for those marked with an asterisk which were done with a Fisher's exact test.