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Directed seed dispersal by scatter-hoarding rodents into areas with a low density of conspecific seeds in the absence of pilferage

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Some species of scatter-hoarding rodents direct seed dispersal by dispersing seeds into areas where the densities of conspecific trees are low. This behavior seems to be an immediate response to cache pilferage and is accomplished by multiple movements. We evaluated whether this directed dispersal also occurs when the scatter-hoarding rodents *Maxomys surifer* disperse seeds away from parent trees when no pilferage has occurred. We simulated parent trees by releasing seeds at different sites in semi-natural enclosures, which prevent pilferage, in Xishuangbanna region, Southwest China. We found that *M. surifer* preferred to disperse seeds into areas with fewer conspecific seeds and that seeds cached in areas of low seed density were more likely to survive than those in areas of high density. Our results indicate that *M. surifer* could provide directed dispersal when they initially disperse seeds away from parent trees, without pilferage. This finding suggests that directed seed dispersal is not an immediate response after pilferage, but an instinctive behavior to reduce the potential for density-dependent cache pilferage. Further, our study indicates that directed seed dispersal is important to mast-seeding plants or species whose seeds are unlikely to be dispersed several times by scatter-hoarding animals.

Key words: density dependence, directed dispersal, pilferage, scatter-hoarding rodents, seed dispersal, Xishuangbanna

Seed-dispersing animals regenerate many plant species by dispersing seeds away from the parent trees (Howe and Smallwood 1982; Smith and Reichman 1984; Vander Wall 1990). Some of these animals also can disperse seeds non-randomly to favorable sites where seeds are more likely to establish and survive, known as directed dispersal (Howe and Smallwood 1982; Wenny 2001). Typical examples of directed dispersal include mistletoe dispersal by birds, dispersal of elaiosome-bearing seeds by ants, and scatter hoarding by corvids (reviewed in Wenny 2001).

Recently, a number of studies have shown that scatter-hoarding rodents also could provide directed dispersal. For example, Briggs et al. (2009) found that small rodents preferred to cache seeds in favorable microsites and at a depth where the emergence or survival of seedlings would be enhanced. Yi et al. (2013) reported that Siberian chipmunks (*Tamias sibiricus*) preferred to cache acorns in moist soils favorable for establishment. Hirsch et al. (2012) found that agoutis (*Dasyprocta punctata*) direct dispersal of *Astrocaryum standleyanum* palm seeds by dispersing the seeds into areas where conspecific densities were lower, thereby reducing the density-dependent theft of cached seeds. Several other studies also found that scatter-hoarding animals preferred to disperse seeds to specific microsites (e.g., an open area) to reduce cache pilferage (Munoz and Bonal 2011; Steele et al. 2014, 2015).

Escaping density-dependent mortality and increasing the colonization of new habitats are key benefits of seed dispersal (Janzen 1970; Connell 1971; Howe and Smallwood 1982; Vander Wall 1990). Consequently, effective seed dispersal requires the deposition of seeds not only far from their own parent trees but also far from other conspecific adult trees. Scatter-hoarding rodents could disperse seeds into areas with low densities of conspecific trees (Munoz and Bonal 2011; Hirsch et al. 2012), which in turn may reduce density-dependent mortality of seeds and seedlings. This behavior could be an immediate response to pilferage of caches, aiming to reduce density-dependent theft of cached seeds (Munoz and Bonal 2011), and it is accomplished by multiple attempts to re-cache seeds. Pilferage is higher around parent trees owing to higher seed abundance attracting more foragers (Munoz and Bonal 2011). Despite this, it is unclear whether directed dispersal occurs in the absence of pilferage.

Recent studies found that most seedlings were from the primary caches (Vander Wall 2002; Xiao et al. 2013; Cao et al. 2016). Typically, small seeds are not dispersed multiple times by scatter-hoarding animals (Vander Wall 2002; Xiao et al. 2004, 2005a, 2005b; Cao and Guo 2011; Wang et al. 2012), although a few studies suggested that rodents could disperse seeds up to 36 times in a tropical forest (Hirsch et al. 2012; Jansen et al. 2012). As a result, it would be most beneficial to the parent tree if dispersal occurs directly into areas of low conspecific density.

Regeneration of seedlings usually occurs in years of high seed abundance for mast-seeding plants (Silvertown 1980; Kelly 1994; Vander Wall 2001, 2002; Yi et al. 2011). In a mast-seeding year, high seed abundance can satiate seed predators and benefit seed survival. Further, seeds usually are dispersed a shorter distance and survive longer in mast-seeding years (Jansen et al. 2004; Xiao et al. 2005a, 2013), because of a lower pilferage rate in these years (Moore et al. 2007). Ultimately, the establishment of seedlings is usually accompanied by lower pilferage rate. Consequently, the question remains whether scatter-hoarding rodents still tend to disperse seeds far from conspecific trees in mast-seeding years when pilferage is low or even non-existent.

We simulated seed dispersal by scatter-hoarding rodents in semi-natural enclosures (simulating focus trees and neighboring conspecific trees) in the Xishuangbanna region, Southwest China. The semi-natural enclosure experiments prevented pilferage. We aimed to investigate whether scatter-hoarding animals provided directed seed dispersal by dispersing seeds into areas with low conspecific tree density when they initially disperse seeds away from parent trees, even when no pilferage occurs.

Materials and Methods

Study site and study species.—The study was carried out in a tropical area in the Xishuangbanna Prefecture, Yunnan Province, China. The average annual rainfall is approximately 1,500 mm, with 80% of the annual rainfall occurring during the wet season (May–October) and 20% falling in the dry season (November–April—Cao and Zhang 1997). The primary vegetation in Xishuangbanna can be divided into 4 types: tropical rain forest, tropical seasonal moist forest, tropical montane evergreen broad-leaf forest, and tropical monsoon forest (Zhu 2006). The tropical montane evergreen broad-leaf forest and tropical rain forest are the predominant vegetation types in this region.

In the study area, *Niviventer confucianus* and *Maxomys surifer* are the dominant rodent species (Wang et al. 2014; Cao et al. 2017). Previous studies found that the predominant behavior of *M. surifer* was scatter hoarding; *N. confucianus* showed some scatter hoarding, but more commonly exhibited larder hoarding (Cao et al. 2011a, 2011b; Wang et al. 2014). We used *M. surifer* as the experimental animal because this was the only species in the study site that exhibited predominantly scatter-hoarding behavior.

The seeds used in this study are from the *Castanopsis hystrix* tree, a dominant species in the tropical montane evergreen broad-leaf forest (Zhu 2006). This species showed marked mast-seeding in the study site (L. Cao, pers. obs.). The fresh seed mass of *C. hystrix* is 0.93 ± 0.04 g (mean ± *SE*), with a coat thickness of 0.34 ± 0.01 mm (mean ± *SE*), and a low tannin content of 0.15% (Wang et al. 2014). Previous studies found that all rodent species in the study site had a preference to depredate and hoard *C. hystrix* seeds (Wang et al. 2014). As a result, these seeds were suitable for investigating the predation and hoarding behavior of scatter-hoarding rodents. We collected seeds from the forest during the fruiting time in November 2012 and then stored them (mixed with dry sand) at 4°C for later use.

Enclosure experiments.—We captured rodents by using live traps made of steel wire mesh (14 × 14 × 30 cm—Chang et al. 2009), baited with shelled peanuts and *Pittosporopsis kerrii* seeds. Species, body mass, and reproductive status of captured rodents were recorded. Adult *M. surifer* individuals were taken to the laboratory for use in enclosure experiments. Pregnant or juvenile individuals were immediately released back into the field. All animals were kept in individual cages (40 × 30 × 25 cm) and provided with adequate food, water, and nest materials. A photoperiod cycle of 12:12 h (light:dark) was maintained. Animals were acclimatized in the laboratory for a minimum of 1 week prior to experimental trials.

Experiments were conducted in 8 semi-natural enclosures (10 × 10 m, with 1.5-m walls—see Wang et al. 2014 for details) from February to August 2013. During the enclosure experiments, 1 animal was placed in the enclosure for observation at a time. The animal was provided with laboratory food on the 1st day to ease acclimation to the new environment. On the 2nd day, 50 tagged *C. hystrix* seeds were placed at the center of the enclosure, simulating seeds from focal trees, and 2 groups of seeds (each group containing 50 tagged *C. hystrix* seeds) were placed in different corners of 1 side of the enclosure, simulating seeds from neighboring conspecific trees (Fig. 1). Seeds were marked by attaching a small, coded plastic tag to each seed by a thin steel thread (Zhang and Wang 2001; Xiao et al. 2006). The plastic tags may provide obvious records of cached seeds to any potential pilferer. However, our study was conducted in the semi-natural enclosure, and no pilferer existed.

During the experiments, we also conducted a comparison study to investigate whether the underground burrow had an effect on hoarding behavior of rodents. For 15 individuals (6 females and 9 males), the seeds simulating neighboring conspecific trees were placed at the side near the underground burrow (Experiment A; Fig. 1a), and for the other 14 individuals (5 females and 9 males), the seeds simulating neighboring

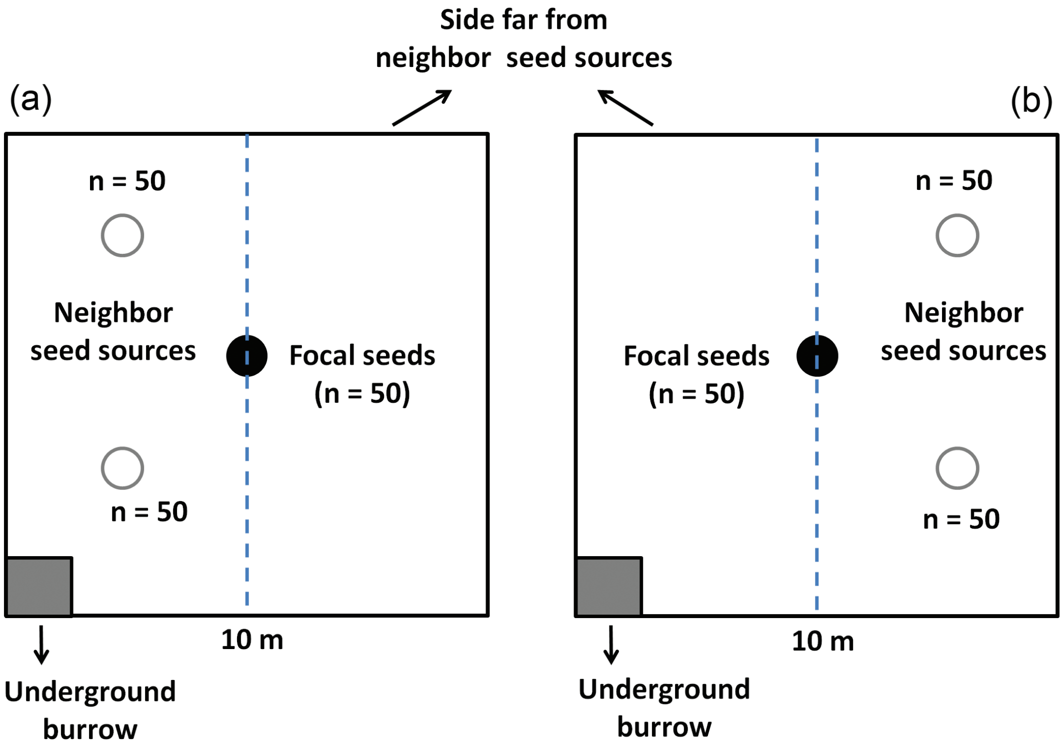

Fig. 1.—Diagram of the semi-natural enclosure and location of focal seeds (black circle) and seeds simulating conspecific trees (white circles). The seeds simulating neighboring conspecific trees were placed at the side a) close to or b) far from the underground burrow.

conspecific trees were placed far from the underground burrow (Experiment B; Fig. 1b).

From the 3rd day, we recorded the fate of each seed as at the seed station or removed (eaten, scatter hoarded, recovered, or missing) every day until most seeds were consumed. The endpoint of the experimental trial was determined when less than 10 seeds remained in the caches and seed stations (including focal seeds and seeds simulating neighboring conspecific trees), or missing seeds had been dispersed to underground burrows. The experiment lasted 5–16 days for each individual. We did not check the seeds that were dispersed into the underground burrow until the experiment had finished to avoid disturbing the hoarding behavior of the rodents.

This study followed guidelines of the American Society of Mammalogists (Sikes et al. 2016) and was approved by the administrative panel on the ethics of animal experiments at Xishuangbanna tropical botanical garden, Chinese Academy of Sciences (Permit Number: XTBG2013-002). After the experiments were finished, all rodents were released at the site where they were captured.

Data analysis.—A generalized linear mixed model (GLMM, in package *lme4*) was used to analyze the probability of seed removal and scatter hoarding with a binomial distribution and logit-link function using R version 3.3.2 (R Development Core Team 2017). Fixed effects were experimental treatment (i.e., A or B), sex, and their interaction. The rodent ID was treated as a random effect. A GLMM also was used to test the difference of the probabilities of seed scatter hoarding and seed survival between the low-seed-density area (i.e., far from neighboring conspecific seed sources) and the high-seed-density area (i.e., close to neighboring conspecific seed sources), and rodent ID was treated as a random effect. A Cox regression model (in the *survival* package in R) was used to compare the difference in survival time between the seeds cached in the low-seed-density areas and the ones in the high-seed-density areas.

RESULTS

All released seeds were harvested (eaten or removed from the seed stations) by rodents during the experiments. We found 77.1 ± 26.1% (mean ± *SD*, $n = 1{,}118$) of the focal seeds and 73 ± 24.7% ($n = 2{,}117$) of the neighboring seeds were removed, and 53.2 ± 29.6% ($n = 771$) and 47.8 ± 28.3% ($n = 1{,}385$) were scatter hoarded, respectively. The experimental treatment, rodent sex, and their interaction showed no effect on the probability of seed removal or scatter hoarding for both focal seeds and neighboring seeds (GLMM, all $P > 0.05$).

In both experiments, the neighboring seeds were more likely to be scatter hoarded near the seed sources (Experiment A, $z = -17.25$, $P < 0.001$; Experiment B, $z = -24.154$, $P < 0.001$), which made the side with the seed sources become a high-seed-density area, while the other side became a low-seed-density area (side far from neighboring seed sources; Figs 1 and 2a). For focal seeds, the probability of seeds being scatter hoarded in the low-seed-density area was significantly higher than that in the high-seed-density area in both experiments (Experiment A, $z = 8.614$, $P < 0.001$; Experiment B, $z = 9.511$, $P < 0.001$; Fig. 2b).

For focal seeds, there was no significant difference between the survival time (defined here as days until eaten)

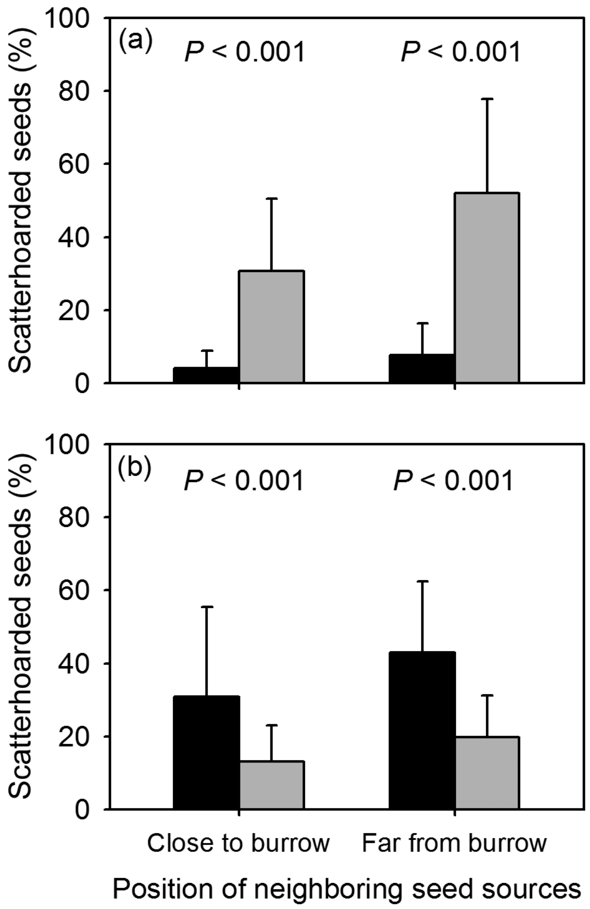

Fig. 2.—The proportion of seeds being scatter hoarded near to (gray bar) or far from (black bar) neighboring conspecific seed sources for a) neighboring seeds and b) focal seeds, when neighboring seed sources were placed on the side close to (Experiment A) or far from (Experiment B) the underground burrow. The horizontal axis represents the location of neighboring seed sources.

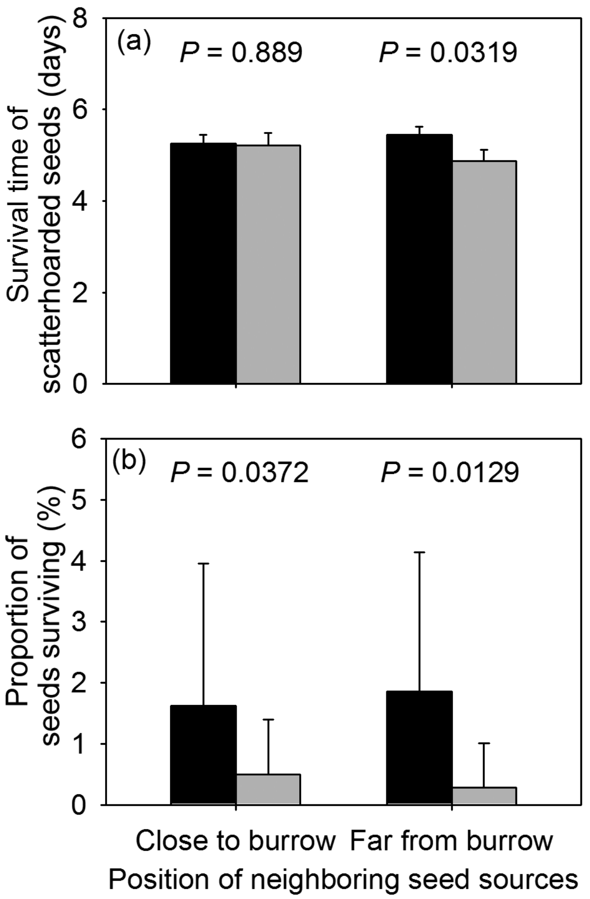

Fig. 3.—Mean survival time (a; mean ± SD) and proportion of surviving to the end of experiment (b) of scatter-hoarded seeds for focal seeds that were cached near to (gray bar) or far from (black bar) neighboring conspecific seed sources, when neighboring seed sources were placed on the side close to (Experiment A) or far from (Experiment B) the underground burrow.

of scatter-hoarded seeds cached in low- and high-seed-density areas in Experiment A (z = 0.139, P = 0.889; Fig. 3a), but the survival time of scatter-hoarded seeds cached in the low-seed-density area was significantly longer than that of the seeds cached in the high-seed-density area in Experiment B (z = −2.145, P = 0.0319; Fig. 3a). At the end of the experiment, many more seeds survived in the area with low seed density than in the area with high density for both Experiment A and B (Experiment A, z = 2.083, P = 0.0372; Experiment B, z = 2.486, P = 0.0129; Fig. 3b).

DISCUSSION

Our study indicates that *M. surifer* provides directed seed dispersal by dispersing seeds into areas with lower densities of conspecific seeds when they initially disperse seeds away from seed stations, even when no cache pilferage exists. This finding suggests that the directed seed dispersal behavior is not an immediate response after caches are pilfered, but an instinctive behavior to reduce the potential for density-dependent cache pilferage. This directed seed dispersal behavior seems critical to mast-seeding plants, as seedling regeneration predominantly occurs in mast-seeding years when pilferage is low. This pattern occurs because animals that pilfer are often also seed hoarders (Vander Wall and Jenkins 2003).

A previous study suggested that some species of scatter-hoarding animals could disperse seeds into areas where the densities of conspecific trees were lower by multiple movements, due to strong pilferage pressure (Hirsch et al. 2012). This cannot be the case for many plant species, especially small-seeded species and mast-seeding species, as their seeds are usually only dispersed a few times by scatter-hoarding animals. Furthermore, recent studies showed that most successfully established seedlings were from primary caches (Vander Wall 2002; Xiao et al. 2013; Cao et al. 2016). Thus, directed dispersal made in the primary-caching process may play a more important role in seed dispersal and seedling establishment than the proposed multiple-caching processes.

In our study, directed dispersal into an area with a low density of conspecific seeds did not increase the mean survival time of scatter-hoarded seeds. However, because there were more caches made from focal seeds in areas away from neighboring seed sources (Fig. 2b), many more seeds ultimately survived in the areas with lower density of conspecific seeds. Hirsch et al. (2012) posited a similar prediction: directed dispersal by dispersing seeds into areas with lower density of conspecific trees will benefit both post-dispersal seed survival and seedling survival. That a low density of conspecific trees may benefit post-dispersal seedling survival also was predicted by the Janzen–Connell hypothesis (Janzen 1970; Connell 1971).

The patterns in seed survival that we detected were due solely to the consumption of seeds cached by our individual study animals in each experimental trial; these individuals made the caches and know where they are. As food supply dwindled during each experimental trial, focal individuals would have to harvest these cached seeds, which may have diminished potential differences in survival between high- and low-seed-density areas that would be seen under more natural conditions. In nature, other conspecifics as well as other species that consume these seeds will be foraging for them. Locating caches by hoarders or other foragers, are concentrating their activity in high-seed-density areas should add to the relative survival prospects for seeds beyond the differences we observed in our semi-natural enclosures.

Whether scatter-hoarding rodents could provide directed seed dispersal has been debated for many years (Wenny 2001; Briggs et al. 2009). Recently, increasingly more studies have reported that scatter-hoarding rodents can provide directed dispersal for plant seeds. For example, scatter-hoarding rodents directed seed dispersal towards favorable microsites and cached at a depth where emergence or survival of seedlings were enhanced (Briggs et al. 2009; Yi et al. 2013). This was considered the 1st form of directed dispersal offered by scatter-hoarding rodents (Hirsch et al. 2012). Burial of seeds that may decrease predation while increasing establishment was considered the 2nd form (Wenny 2001). Hirsch et al. (2012) demonstrated a 3rd form, suggesting that scatter-hoarding rodents disperse seeds towards areas with low densities of conspecific adult trees.

Our study has demonstrated this 3rd form, and further supplied new information that the behavior of dispersing seeds towards areas with low densities of conspecific adult trees is not an immediate response after caches are pilfered, but a behavior based on experience or heredity. We also have shown that this directed dispersal can be accomplished during the initial transportation of seeds away from parent trees by scatter-hoarding rodents. Our findings suggest that this form of directed seed dispersal may be a widespread phenomenon, as predicted by Hirsch et al. (2012).

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Literature Cited

Briggs, J. S., S. B. Vander Wall, and S. H. Jenkins. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. Ecology 90:675–687.

Cao, L., and C. Guo. 2011. Seed dispersal effectiveness of small rodents to the *Castanopsis indica* in Xishuangbanna tropical seasonal rain forest. Acta Theriologica Sinica 31:323–329.

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

Cao, L., Z. S. Xiao, C. Guo, J. Chen, and Z. B. Zhang. 2011a. Scatter-hoarding rodents as secondary seed dispersers of a frugivore-dispersed tree *Scleropyrum wallichianum* in a defaunated Xishuangbanna tropical forest, China. Integrative Zoology 6:227–234.

Cao, L., Z. Xiao, Z. Wang, C. Guo, J. Chen, and Z. Zhang. 2011b. High regeneration capacity helps tropical seeds to counter rodent predation. Oecologia 166:997–1007.

Cao, M., and J. H. Zhang. 1997. Tree species diversity of tropical forest vegetation in Xishuangbanna, SW China. Biodiversity and Conservation 6:995–1006.

Chang, G., Z. Xiao, and Z. Zhang. 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 82:7–11.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–312 in Dynamics of populations (P. J. D. Boer and G. Gradwell, eds.). Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

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

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Reviews of Ecology and Systematics 13:201–228.

Jansen, P. A., F. Bongers, and L. Hemerik. 2004. Seed mass and mast seeding enhance dispersal by a Neotropical scatter-hoarding rodent. Ecological Monographs 74:569–589.

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

Janzen, D. H. 1970. Herbivores and the number of tree species in Tropical forests. The American Naturalist 104:501–528.

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

Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88:2529–2540.

Munoz, A., and R. Bonal. 2011. Linking seed dispersal to cache protection strategies. Journal of Ecology 99:1016–1025.

R Core Team (2017). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.http://www.R-project.org

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14:235–250.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329–351.

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

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

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, 1–445.

Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. The Botanical Review 67:74–117.

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

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

Wang, B., G. Wang, and J. Chen. 2012. Scatter-hoarding rodents use different foraging strategies for seeds from different plant species. Plant Ecology 213:1329–1336.

Wang, Z., L. Cao, and Z. Zhang. 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.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evolutionary Ecology Research 3:51–74.

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

Xiao, Z. S., Z. B. Zhang, and C. J. Krebs. 2013. Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. Journal of Ecology 101:1256–1264.

Xiao, Z. S., Z. B. Zhang, and Y. S. Wang. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. Forest Ecology and Management 195:141–150.

Xiao, Z. S., Z. B. Zhang, and Y. S. Wang. 2005a. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii* (Fagaceae). Plant Ecology 177:249–257.

Xiao, Z. S., Z. B. Zhang, and Y. S. Wang. 2005b. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecologica 28:221–229.

Yi, X. F., G. Q. Liu, M. A. Steele, Z. Shen, and C. Q. Liu. 2013. Directed seed dispersal by a scatter-hoarding rodent: the effects of soil water content. Animal Behaviour 86:851–857.

Yi, X. F., Y. Q. Yang, and Z. B. Zhang. 2011. Intra- and inter-specific effects of mast seeding on seed fates of two sympatric *Corylus* species. Plant Ecology 212:785–793.

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

Zhu, H. 2006. Forest vegetation of Xishuangbanna, south China. Forestry Studies in China 8:1–58.

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