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ORIGINAL ARTICLE

Seed size affects rodent–seed interaction consistently across plant species but not within species: evidence from a seed tracking experiment of 41 tree species

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Abstract

Scatter-hoarding rodents play a crucial role in seed survival and seed dispersal. As one of the most important seed traits, seed size and its effect on rodent–seed interaction attract lots of attention. Current studies usually target one or a few species and show inconsistent patterns; however, few experiments include a large number of species although many plant species usually coexist in natural forest and overlap in fruiting time. Here, we tracked the dispersal and predation of 26 100 seeds belonging to 41 tree species in a subtropical forest for 2 years. Most species showed no relationships between seed size and rodent foraging preference, while the remaining species displayed diverse of patterns: monotonic decrease and increase trends, and hump-shaped and U-shaped patterns, indicating that a one-off study with a few species might give misleading information. However, the seed size effect across species was consistent in both years, indicating that including a large number of species that hold a sufficient range of seed size may avoid the aforementioned bias. Interestingly, seed size effect differed among rodent foraging processes: a negative effect on seed harvest, a hump-shaped effect on seed removal and removal distance, while a positive effect on overwinter survival of cached seeds, indicating that rodents may make trade-offs between large and small seeds both among foraging processes and within a single process, thus lead to a parabolic relationship between seed size and seed dispersal success, that is medium-sized seeds were more likely to be removed and cached, and transported with a further distance.

Key words: foraging preference, plant–animal interaction, scatter-hoarding, seed dispersal, seed predation

INTRODUCTION

Many small mammals, especially rodents, are believed to play a crucial role in seed survival and seedling establishment which in turn influence the diversity and structure of plant community in many ecosystems, especially forests; because they can act as both seed predators and dispersers during their scatter-hoarding processes

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(Vander Wall 2010; Hirsch *et al*. 2012; Cao *et al*. 2016; Zhang *et al*. 2021). When rodents encounter a seed, they usually have a series of step-wise decisions to make: harvest the seed or ignore it; if choose to harvest the seed, consume it *in situ* or transport it to some other places; upon transportation, where and how far; and consume the seed or hoard it for later use after transporting (Wang *et al*. 2013; Wang & Ives 2017). Seed traits are essential factors in determining the foraging preference of scatter-hoarding rodents, thus in turn influence seed fate (Wang & Chen 2009; Vander Wall 2010; Zhang *et al*. 2016; Lichti *et al*. 2017).

As one of the most important seed traits, seed size and its effect on seed predation and dispersal by rodents have been attracted lots of attentions; however, current studies often show inconsistent results (Blate *et al*. 1998; Moles *et al*. 2003; Wang & Chen 2009; Cao *et al*. 2016; Chen *et al*. 2021). How to explain these inconsistent patterns? In general, seed size has 2 opposite effects on the foraging behavior of scatter-hoarding rodents: on the one hand, seed size is usually positively related to the absolute energy content of a seed (Gong *et al*. 2015; Wang *et al*. 2016), and rodents prefer larger seeds because of their higher energy content compared to smaller ones (Wang & Chen 2009). On the other hand, larger seeds usually require more handling time and energy inputs (especially during the seed transporting and caching processes) that may in turn increase foraging risk and decrease foraging efficiency (Munoz & Bonal 2008). By using artificial seeds, Wang *et al*. (2013) found that the preference of larger seeds was limited within a threshold, beyond which rodents would prefer the smaller ones, indicating that the effects of seed size on rodent preference may be contingent on the range of seed size available. Lots of evidences seem to support this prediction that rodent foraging preference can be positive (Jansen *et al*. 2004; Wang & Chen 2009), negative (Blate *et al*. 1998) or independent related with seed size (Moles *et al*. 2003; Gong *et al*. 2015), even some complex non-monotonic patterns (Cao *et al*. 2016; Dylewski *et al*. 2020).

Current studies testing the seed size effect on scatter-hoarding rodents' foraging preference often conduct their experiment at the population level by focusing on a single plant species (Jansen *et al*. 2004; Xiao *et al*. 2005; Cao *et al*. 2016; Wang & Ives 2017). While in natural forest, diverse of plant species coexist, and their fruiting time often overlaps (Li *et al*. 2012; Sunyer *et al*. 2014). Therefore, one question may be asked: how seed size affects rodents' foraging behavior at the multiple species level? Blate *et al*. (1998) showed a negative relationship between seed size and the proportion of seed harvest among 40 species in a tropical forest, while Gong *et al*. (2015) showed no correlation between seed size and seed harvest by studying 30 species in an alpine pine forest. The energy cost may differ among processes of the scatter-hoarding behavior, and rodents may show different preferences upon seed size among processes (Wang *et al*. 2013). However, few studies that involve a large number of species have been conducted to test the seed size effects on the following processes after seed harvest, for example seed removal, caching and dispersal distance; it is therefore difficult to do a reliable statistical analysis among species. Studies compiling data from different experiments provide a way to explore this question. For example, Zhang *et al*. (2016) compiled a dataset including 23 tree species collected from 4 study sites spanning 23° of latitude, and their results showed that seed size was negatively correlated with the proportion of seeds both eaten *in situ* and eaten after removal, but positively correlated with the proportion of larder hoarded. By compiling data from published papers, Thomson *et al*. (2011) found no significant relationship between seed size and dispersal distance across 24 plant species that depended on scatter-hoarding animals for seed dispersal. However, different studies often differ in environmental factors, experimental protocols, seed availability, and abundance and composition of rodent community, all of which play important roles on rodent–seed interaction (Xiao *et al*. 2013; Garzon-Lopez *et al*. 2015; Yang *et al*. 2020; Wang 2020a; Zeng *et al*. 2021), and thus may potentially bias the patterns from compiling dataset.

In order to get a more comprehensive understanding of seed size effects on rodents' scatter-hoarding behavioral processes among species, we tracked the dispersal and predation of 26 100 seeds belonging to 41 tree species in a subtropical forest for 2 consecutive years. We wanted to answer the following questions: (1) does seed size affect rodent foraging preference across plant species; if so, is there a consistent pattern of seed size effect among scatter-hoarding processes? (2) Does seed size affect rodents' foraging preference within each single species; if so, do the species follow a same rule? (3) Do the above 2 predictions show similar patterns between years?

MATERIALS AND METHODS

Study site

The field experiments were conducted in 2017 and 2018 in a subtropical evergreen broad-leaved forest in Ailao Mountains in Yunnan province, southwestern China (24°32′N, 101°01′E, altitude 2045 m). The mean annual temperature is 11.7°C, and annual precipitation is 1923.1 mm, much of which occurs in the wet season (from May to October). The dominant tree species in the forest are Fagaceae species. Small rodents were primarily response for the seed predation and dispersal of our experimental seeds (unpublished camera trap data), and the dominant species were Chinese white-bellied rat (*Niviventer confucianus*), large white-bellied rat (*Niviventer excelsior*) and *Apodemus ilex*. The rodent abundance differed between years, with the trap success being 6.5% in 2017 and 12.2% in 2018 ($n = 245$ trap days), respectively.

Study species

In order to guarantee both a sufficient sample size of plant species and a large interspecific variation in seed size, 41 tree species of seeds were bought from Seed and Seedling Company of Yunnan to do the seed tracking experiments: 28 species in 2017 and 30 species in 2018, with 17 species being used in both years. Seed size varied among species in both years: from 0.01 to 10.43 g with the mean value being 0.85 ± 1.07 g (±SD) in 2017 and from 0.01 to 11.13 g (0.79 ± 1.07 g) in 2018.

The seeds used in this study were not collected directly from the focused forest; however, we do not think it would bias our target question (i.e. effects of seed size on foraging preference of scatter-hoarding rodents); because: (1) all the 41 tree species are either native species that distribute widely in our study area or nearby regions, or introduced species that have been used for afforestation for decades (Feng *et al*. 2021); therefore, rodents in our study forest have been already familiar with the experimental species of seeds; (2) rodents can identify tiny differences in seed traits, no matter the seeds are local or introduced (or exotic) species, even artificial seeds made from clay and peanut powder (Wang & Chen 2009; Gong *et al*. 2015; Wang 2020a; Thein *et al*. 2021); (3) our previous study showed that both local and introduced plant species of seeds suffered similar predation by rodents (Gong *et al*. 2015); and (4) seed size also showed similar effects on the probability of seed removal by small mammals among both local and exotic species (Dylewski *et al*. 2020).

Based on our live-trap and camera-trap surveys, rodents were the main predators and dispersers of our experimental seeds. It would be very difficult for invertebrates to open the seeds as most of them held very hard seed coats, and we found few invertebrate seed predator at the seed releasing points or nearby. More importantly, the seed fragments found at the releasing points showed strong evidence of predation by granivorous rodents. Furthermore, by using the same seed species, we studied the seed predation and dispersal in several other forests (including both temperate and tropical forests), and found that the seeds were seldom predated by other seed predators, such as ants and birds (Wang & Yang 2007; Gong *et al*. 2015; Wang 2020a; Thein *et al*. 2021).

Seed tracking experiment

Three 50 m × 50 m plots were established in the forest with at least 150 m apart from each other. At each plot, 36 seed releasing points were established in a 6 × 6 grids, about 10 m between points. Each seed was weighted and drilled a small hole (∼ 0.6 mm) at the base part and connected with a 3.5 cm × 2.5 cm plastic tag by a 15 cm long steel line (0.2 mm in diameter), and each tag was numbered for individual seed identification (Xiao *et al*. 2006a; Wang & Ives 2017). Tags was proved to have little effect on the probability of seeds being eaten or dispersed by rodents (Zhang & Wang 2001; Xiao *et al*. 2004; Wang *et al*. 2012; but see Wrobel & Zwolak 2013). Tags may affect the cache recover, especially by a naive rodent if it has experience in locating caches by tags; however, Xiao *et al*. (2006a) showed that tags had little effect on cache survival. In this study, the seed mass differed greatly among species, with the range being 0.01–11.13 g, while the wire and tag attached on each seed was about 0.25 g. Therefore, the tag effect may differ among different sized seeds. For example, tags could make small seeds less valuable by increasing their handling costs more than that for large seeds. Conversely, the tags could also make it easier for rodents to locate small seeds once they learn that the tags are associated with a food reward. However, few experiments have been conducted to test the tag effect among different sized seeds. Nevertheless, the tag tracking method has been widely used to study seed dispersal by scatter-hoarding rodents of many plant species, with the seed mass ranging from 0.01 to 60 g (Jansen *et al*. 2004; Wang *et al*. 2012; Lai *et al*. 2014; Yadok *et al*. 2020), and almost all of our experimental seeds fell into this range.

The seed tracking experiment was conducted right after the fruiting season to stagger the potential effects of local seed production. In 2017, 12 600 seeds (450 seeds × 28 species) were selected and released into the 3 plots for 15 consecutive times every 6 days, with 840 seeds being released each time (10 seeds × 28 species × 3 plots). At each time, 28 releasing points were randomly selected from the 36 points at each plot, and 1 species was randomly assigned to each point, and then 10 seeds of the selected species were released at the point. In 2018, 13 500 seeds (450 seeds × 30 species) were released following the same procedure.

In this study, we mainly focused on the effect of seed size on the final seed fate. From the plant aspect, the final seed fate, especially the seeds dispersed successfully (i.e. overwinter survival of cached seeds), directly determines the following seedling regeneration. Therefore, for both seed tracking experiments, the overwinter fate of each seed was checked in May of the following year, while the intermediate scatter-hoarding processes (e.g. cache recovery and multiple re-caching) were not surveyed. During the seed fate survey, we did a complete search around each point with the radius being 30 m. Furthermore, we also haphazardly searched beyond this area to relocate as many of the dispersed seeds as possible. Seed fates were first divided into ignored (i.e. seeds that were left intact at their original releasing points) and harvested by rodents. The harvested seeds included seeds eaten *in situ* (i.e. seeds that were consumed at their original points) and seeds removed by rodents. The removed seeds included seeds dispersed successfully (i.e. seeds deposited intact on the ground or buried in the soil after being removed), seeds eaten after being transported and missing seeds (seeds that were not found within our search area with their fates unknown) (Wang *et al*. 2013; Wang & Yang 2014; Wang & Ives 2017). When a removed seed was found, we measured the dispersal distance to its original releasing point. After the seed fate survey, all the experimental seeds and fragments were taken back to the laboratory.

Data analysis

All the statistical analyses were conducted in R (version 3.6.1). A generalized linear mixed model (GLMM) was used to analyze the effect of seed size on seed fates (including the probability of seeds being ignored versus harvested by rodents, probability of being eaten *in situ* versus removed by rodents and eaten versus dispersed after being removed), with a binomial error distribution and logit link function (function *glmer*, package "lme4"). A linear mixed model was used to analyze the seed size effect on dispersal distance that was log-transformed to reduce skewness (function *lmer*, package "lme4"). First, we analyzed all the species together, considering seed releasing point nested in plot, species and time of seeds released as the random effects. Second, we run the same models to analyze each species separately, with seed releasing point nested in plot and time of seeds released being the random effects. Each of the above analysis included 2 candidate models: (1) Model I, the seed predation and dispersal indexes were predicted to monotonically increase or decrease with seed size, and seed size was treated as a fixed factor; and (2) Model II, a unimodal relationship was predicted between the seed predation and dispersal index and seed size, so both seed size and the quadratic term of seed size were included as fixed factors. The better fitting model was selected under the most-parsimonious criterion and Akaike information criterion (AIC) (function *anova*, package "stats"). Because the same test was repeated for each species, the false discovery rate was used to adjust the P values to avoid a type I error (function *p.adjust*, package "stats").

RESULTS

Seed harvest

In 2017, 63.0% of the 12 600 released seeds were harvested by rodents. A marginally significant relationship was detected between seed size and the probability of seeds being harvested with the result that smaller seeds were more likely to be harvested than larger ones across species (generalized linear mixed model, $z = -1.72$, $P = 0.086$; Fig. 1a). The proportion of seeds harvested differed among the 28 species, ranging from 7.8% to 100%. When analyzing each of the 28 species separately, none species showed a significant correlation between seed size and the probability of seeds being harvested (including 1 species with all the seeds being harvested) (Table 1).

In 2018, 71.2% of the 13 500 seeds were harvested. Although the model including the quadratic term of seed size was selected based on AIC (seed size, $z = -3.36$, $P = 0.001$; seed size^2, $z = 2.83$, $P = 0.005$), the overall pattern showed a clear negative relationship between seed size and the probability of seed harvest (Fig. 1b). The proportion of seeds harvested differed among the 30 species, ranging from 3.8% to 100%. Finally, 1 species showed a similar negative effect of seed size on seed harvest as the overall pattern across species, 1 species showed a hump-shaped pattern (i.e. medium sized seeds were more likely to be harvested than both small and large ones), 1 species showed a U-shaped pattern, and the remaining 27 species showed no effect of seed size on the probability of seeds being harvested (including 2 species with all the seeds being harvested) (Table 2).

Seeds removed versus eaten *in situ*

Of the 7939 harvested seeds in 2017, 57.8% were eaten *in situ*, while 42.2% were removed by rodents. A hump-shaped pattern was detected between seed size and the probability of seeds being removed, indicating that

Table 1 Relationship between seed size and the probability of seeds being harvested, removed and dispersed successfully, and dispersal distance for each of the 28 species in 2017

	Harvest			Removal			Successfully dispersed			Distance
Species	Mean ± SD	%	#	Mean ± SD	%	#	Mean ± SD	%	#	*
Ligustrum delavayanum	0.06 ± 0.03 (0.01–0.31)	90.7	—	0.06 ± 0.03 (0.01–0.31, 408)	13.0	—	0.05 (1)	100		
Ophiopogon bodinieri	0.10 ± 0.05 (0.01–0.55)	71.3	—	0.10 ± 0.05 (0.01–0.55, 321)	17.1	—	0.10 ± 0.04 (0.06–0.15, 4)	0		
Kadsura coccinea	0.13 ± 0.03 (0.06–0.20)	90.2	—	0.13 ± 0.03 (0.06–0.20, 406)	15.0	—	0.14 ± 0.03 (0.11–0.19, 8)	0	—	—
Cedrus deodara	0.13 ± 0.04 (0.02–0.35)	82.7	—	0.13 ± 0.04 (0.04–0.35, 372)	14.8	—	0.16 ± 0.09 (0.08–0.34, 7)	14.3	—	—
Sapium sebiferum	0.16 ± 0.04 (0.07–0.44)	42.7	—	0.16 ± 0.04 (0.09–0.44, 192)	49.0	—	0.17 ± 0.04 (0.12–0.27, 12)	16.7	↗	—
Ardisia crenata	0.20 ± 0.04 (0.05–0.37)	12.0	—	0.20 ± 0.050 (0.11–0.37, 54)	31.5	—	0.18 ± 0.07 (0.13–0.23, 2)	50.0		
Osmanthus sp.	0.20 ± 0.05 (0.03–0.52)	98.7	—	0.20 ± 0.06 (0.03–0.52, 444)	25.7	—	0.22 ± 0.04 (0.14–0.32, 30)	6.7	—	—
Prunus cerasoides	0.25 ± 0.05 (0.09–0.44)	60.7	—	0.26 ± 0.05 (0.12–0.44, 273)	71.1	↗	0.27 ± 0.05 (0.19–0.44, 57)	14.0	—	—
Diospyros kaki	0.27 ± 0.04 (0.10–0.42)	29.8	—	0.27 ± 0.04 (0.10–0.35, 134)	59.0	—	0.26 ± 0.04 (0.19–0.32, 11)	36.4	↗	—
Chimonanthus praecox	0.27 ± 0.17 (0.06–1.87)	75.8	—	0.28 ± 0.20 (0.08–1.87, 341)	22.3	—	0.26 ± 0.07 (0.17–0.44, 21)	14.3	—	—
Bauhinia sp.	0.29 ± 0.07 (0.08–0.51)	98.4	—	0.29 ± 0.06 (0.12–0.51, 443)	29.1	—	0.31 ± 0.06 (0.23–0.43, 23)	0	—	—
Chionanthus retusus	0.32 ± 0.06 (0.19–0.79)	94.2	—	0.32 ± 0.06 (0.19–0.79, 424)	52.6	∩	0.34 ± 0.09 (0.25–0.79, 58)	24.1	—	—
Pinus armandii	0.34 ± 0.06 (0.12–0.58)	98.0	—	0.34 ± 0.06 (0.12–0.58, 441)	44.2	↗	0.35 ± 0.05 (0.27–0.50, 46)	8.7	—	—
Ormosia yunnanensis	0.37 ± 0.07 (0.16–0.60)	73.6	—	0.37 ± 0.07 (0.16–0.60, 331)	19.3	—	0.38 ± 0.10 (0.16–0.52, 10)	0	—	—
Castanopsis fleuryi	0.46 ± 0.14 (0.13–0.85)	96.4	—	0.46 ± 0.14 (0.13–0.85, 434)	33.4	↗	0.49 ± 0.13 (0.24–0.85, 39)	10.3	—	—

(*Continued*)

Table 1 (Continued)

	Harvest			Removal			Successfully dispersed			Distance
Species	Mean ± SD	%	#	Mean ± SD	%	#	Mean ± SD	%	#	∗
Delonix regia	0.47 ± 0.09 (0.20–0.71)	98.7	—	0.47 ± 0.09 (0.20–0.71, 444)	28.6	↗	0.48 ± 0.07 (0.34–0.65, 29)	3.4	—	↗
Pinus koraiensis	0.66 ± 0.34 (0.18–3.35)	100	—	0.66 ± 0.34 (0.18–3.35, 450)	51.8	∩	0.61 ± 0.15 (0.18–0.93, 59)	18.6	—	∪
Phoenix dactylifera	0.72 ± 0.16 (0.39–1.63)	63.8	—	0.70 ± 0.13 (0.39–1.45, 287)	81.5	—	0.67 ± 0.14 (0.40–0.94, 38)	21.1	—	—
Wisteria sp.	0.74 ± 0.21 (0.24–1.56)	28.2	—	0.73 ± 0.19 (0.35–1.21, 127)	29.9	—	0.73 ± 0.24 (0.50–1.21, 8)	0	—	—
Tectona grandis	0.82 ± 0.22 (0.25–1.57)	16.0	—	0.83 ± 0.21 (0.40–1.31, 72)	62.5	—	0.88 (1)	100		
Erythrophleum fordii	1.03 ± 0.15 (0.29–1.47)	52.0	—	1.01 ± 0.18 (0.01–1.38, 234)	15.4	—	0.99 ± 0.21 (0.74–1.17, 4)	50.0		
Melia azedarach	1.29 ± 0.48 (0.24–3.29)	7.8	—	1.30 ± 0.62 (0.25–2.70, 35)	91.4	—	1.50 ± 0.85 (0.90–2.1, 2)	100		
Lysidice rhodostegia	1.44 ± 0.27 (0.09–2.24)	98.7	—	1.43 ± 0.27 (0.09–2.24, 444)	73.9	—	1.45 ± 0.23 (0.89–2.03, 70)	4.3	—	—
Sapindus mukorossi	1.48 ± 0.29 (0.33–2.46)	59.6	—	1.48 ± 0.27 (0.71–2.46, 268)	70.1	—	1.53 ± 0.25 (0.89–1.95, 34)	23.5	—	—
Amygdalus davidiana	1.72 ± 0.43 (0.09–3.50)	10.2	—	1.64 ± 0.49 (0.09–2.62, 46)	100	—	1.90 (1)	0		
Choerospondias axillaris	2.70 ± 0.58 (1.40–4.99)	9.3	—	2.78 ± 0.60 (1.79–4.68, 42)	97.6	—	2.64 ± 0.16 (2.53–2.82, 3)	100		
Pyrularia edulis	2.72 ± 0.74 (0.61–4.57)	94.9	—	2.72 ± 0.73 (0.75–4.57, 427)	97.0	—	2.65 ± 0.71 (0.75–3.98, 38)	23.7	—	—
Davidia involucrata	4.51 ± 1.45 (1.79–10.43)	10.0	—	4.45 ± 1.17 (2.08–6.85, 45)	68.9	—	— (0)			

The mean seed sizes (± SD) and the proportion (%) of released seeds being harvested, the proportion of harvested seeds being removed and the proportion of removed seeds being dispersed successfully (excluding the missing seeds) are shown in the table. The numbers in parentheses are the minimum and maximum seed sizes and the sample sizes (i.e. number of seeds analyzed in the model); while for seed harvest, the total number of seeds released for each species is 450. #The statistical analysis is based on the generalized linear mixed model; ∗The statistical analysis is based on the linear mixed model. ∩: hump-shaped; ∪: U-shaped; ↗: positive linear correlation; ↘: negative linear correlation; —: Means no correlation (including the species that were not statistically analyzed because almost all the seeds were either success (1) or failure (0); and blank: not statistically analyzed because of the small sample sizes.

Table 2 Relationship between seed size and the probability of seeds being harvest, removed and dispersed successfully, and dispersal distance for each of the 30 species in 2018

	Harvest			Removal			Successfully dispersed			Distance
Species	Mean ± SD	%	#	Mean ± SD	%	#	Mean ± SD	%	#	*
Prunus serrula	0.06 ± 0.02 (0.01–0.16)	99.6	—	0.06 ± 0.02 (0.01–0.16, 448)	6.7	∪	0.06 ± 0.04 (0.01–0.16, 12)	0	—	—
Leucaena leucocephala	0.06 ± 0.02 (0.01–0.14)	88.9	—	0.06 ± 0.02 (0.01–0.14, 400)	10.3	∩	0.06 ± 0.02 (0.01–0.08, 18)	5.6	—	—
Taxus wallichiana	0.07 ± 0.02 (0.01–0.13)	97.1	—	0.07 ± 0.02 (0.01–0.13, 437)	7.6	—	0.07 ± 0.03 (0.02–0.11, 22)	0	—	—
Pistacia weinmannifolia	0.09 ± 0.03 (0.01–0.17)	99.8	∪	0.09 ± 0.03 (0.01–0.17, 449)	15.1	—	0.09 ± 0.03 (0.02–0.14, 30)	0	—	—
Koelreuteria paniculata	0.11 ± 0.03 (0.02–0.32)	99.6	—	0.11 ± 0.03 (0.02–0.32, 448)	26.6	↗	0.13 ± 0.04 (0.05–0.32, 43)	14.0	∩	∩
Diospyros lotus	0.14 ± 0.03 (0.04–0.23)	31.3	—	0.15 ± 0.03 (0.06–0.23, 141)	52.5	—	0.15 ± 0.03 (0.10–0.19, 26)	3.8	↗	—
Cinnamomum sp.	0.15 ± 0.03 (0.05–0.24)	99.8	—	0.15 ± 0.03 (0.05–0.24, 449)	37.4	↗	0.15 ± 0.03 (0.09–0.22, 96)	6.3	—	—
Sapium sebiferum	0.16 ± 0.03 (0.08–0.37)	46.9	—	0.16 ± 0.03 (0.08–0.24, 211)	47.9	—	0.17 ± 0.03 (0.11–0.22, 61)	47.5	—	—
Sophora japonica	0.17 ± 0.06 (0.03–0.38)	54.0	↘	0.17 ± 0.06 (0.03–0.33, 243)	36.2	↗	0.18 ± 0.06 (0.05–0.31, 56)	0	—	—
Parakmeria yunnanensis	0.18 ± 0.04 (0.03–0.29)	95.6	—	0.18 ± 0.04 (0.03–0.29, 430)	72.1	∩	0.18 ± 0.03 (0.08–0.29, 200)	4.5	—	—
Poncirus trifoliata	0.18 ± 0.04 (0.01–0.28)	98.4	—	0.18 ± 0.04 (0.01–0.28, 443)	46.7	↗	0.18 ± 0.03 (0.08–0.28, 130)	0.8	—	—
Osmanthus sp.	0.20 ± 0.06 (0.04–0.57)	99.6	—	0.20 ± 0.06 (0.04–0.57, 448)	35.7	↗	0.22 ± 0.07 (0.09–0.57, 97)	1.0	—	—
Prunus cerasoides	0.24 ± 0.06 (0.11–0.46)	78.9	—	0.24 ± 0.06 (0.11–0.46, 355)	77.2	—	0.24 ± 0.05 (0.15–0.42, 154)	22.1	—	—
Pinus armandii	0.28 ± 0.07 (0.11–0.56)	100.0	—	0.28 ± 0.07 (0.11–0.56, 450)	57.8	—	0.29 ± 0.07 (0.16–0.50, 158)	1.9	—	—
Chionanthus retusus	0.29 ± 0.06 (0.14–0.48)	98.4	—	0.29 ± 0.06 (0.14–0.48, 443)	72.5	↗	0.30 ± 0.06 (0.17–0.48, 184)	14.1	∩	—
Bauhinia sp.	0.31 ± 0.06 (0.11–0.50)	99.1	—	0.31 ± 0.06 (0.11–0.50, 446)	58.3	↗	0.32 ± 0.06 (0.16–0.48, 151)	7.3	—	—
Ormosia yunnanensis	0.37 ± 0.07 (0.18–0.56)	57.8	—	0.37 ± 0.07 (0.21–0.56, 260)	47.3	—	0.37 ± 0.06 (0.23–0.49, 57)	8.8	—	—

(*Continued*)

Table 2 (Continued)

	Harvest			Removal			Successfully dispersed			Distance
Species	Mean ± SD	%	#	Mean ± SD	%	#	Mean ± SD	%	#	*
Delonix regia	0.50 ± 0.10 (0.16–0.76)	99.1	—	0.50 ± 0.10 (0.16–0.76, 446)	64.6	↗	0.52 ± 0.10 (0.23–0.76, 159)	7.5	—	—
Jatropha curcas	0.61 ± 0.15 (0.04–0.97)	32.7	—	0.61 ± 0.15 (0.18–0.95, 147)	55.1	—	0.60 ± 0.14 (0.24–0.84, 30)	46.7	—	—
Phoenix dactylifera	0.70 ± 0.13 (0.36–1.17)	96.7	—	0.70 ± 0.13 (0.36–1.17, 435)	95.2	—	0.70 ± 0.14 (0.40–1.14, 138)	19.6	—	—
Tectona grandis	0.71 ± 0.22 (0.17–1.46)	18.4	—	0.66 ± 0.24 (0.17–1.25, 83)	15.7	—	0.77 ± 0.27 (0.23–1.10, 8)	12.5	—	—
Erythrophleum fordii	1.01 ± 0.18 (0.29–1.38)	32.2	—	0.99 ± 0.20 (0.29–1.38, 145)	73.1	∩	1.02 ± 0.17 (0.43–1.34, 62)	21.0	—	—
Phoenix sylvestris	1.12 ± 0.22 (0.58–2.05)	59.6	—	1.11 ± 0.22 (0.62–2.05, 268)	96.6	—	1.11 ± 0.22 (0.73–2.05, 92)	27.2	—	—
Sapindus mukorossi	1.46 ± 0.30 (0.63–2.50)	91.3	—	1.46 ± 0.30 (0.63–2.50, 411)	97.6	—	1.45 ± 0.29 (0.63–2.22, 167)	38.9	—	—
Lysidice rhodostegia	1.48 ± 0.29 (0.67–2.31)	99.1	—	1.48 ± 0.29 (0.67–2.31, 446)	89.2	—	1.48 ± 0.30 (0.82–2.31, 176)	6.3	—	—
Melia azedarach	1.51 ± 0.56 (0.41–3.20)	3.8	—	1.59 ± 0.56 (0.82–2.58, 17)	88.2	∩	1.52 ± 0.51 (0.94–2.58, 7)	100	—	—
Amygdalus davidiana	1.80 ± 0.44 (0.70–3.76)	22.2	∩	1.74 ± 0.39 (0.70–2.87, 100)	98.0	∩	1.83 ± 0.37 (1.21–2.87, 41)	61	—	—
Torreya sp.	2.13 ± 0.40 (1.04–3.49)	100	—	2.13 ± 0.40 (1.04–3.49, 450)	75.1	↗	2.07 ± 0.39 (1.10–3.08, 113)	0.9	—	—
Choerospondias axillaris	2.63 ± 0.68 (0.94–4.82)	30.4	—	2.57 ± 0.72 (0.94–4.82, 137)	99.3	—	2.55 ± 0.85 (0.94–4.66, 44)	81.8	—	—
Davidia involucrata	4.84 ± 1.52 (1.53–11.13)	4.9	—	4.87 ± 1.72 (2.38–9.04, 22)	100	—	4.49 ± 1.02 (3.04–5.78, 5)	100	—	—

For detailed explanation of the table, please see Table 1.

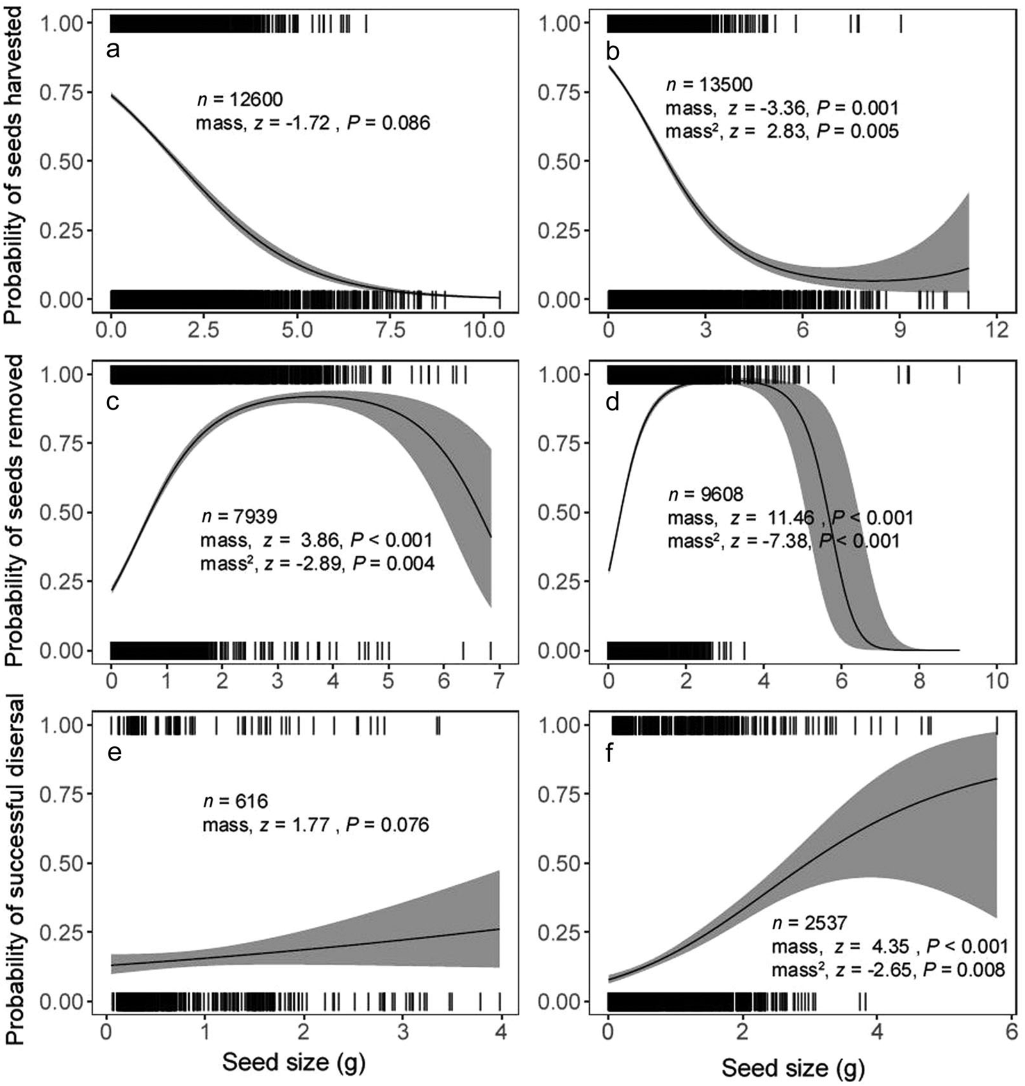

Figure 1 Effects of seed size on the probability of seeds (a, b) being harvested, (c, d) being removed, and (e, f) being dispersed successfully. The regression lines with 95% confidence bands were based on the generalized linear model. The short black lines at the top and bottom of panels represent the seeds that were either success (1) or failure (0), respectively.

medium sized seeds were removed rather than directly consumed *in situ* much more often than both small and large ones (seed size, $z = 3.86$, $P < 0.001$; seed size^2, $z = -2.89$, $P = 0.004$; Fig. 1c). The proportion of seeds removed ranged from 13.0% to 100% among the 28 species. Two species showed a similar hump-shaped pattern, 4 species showed a positive effect of seed size on seed removal (i.e. larger seeds were more likely to be removed) and the remaining 22 species showed no effect of seed size on the probability of seeds being removed (including 1 species with all the harvested seeds being removed) (Table 1).

Of the 9608 harvested seeds in 2018, 45.8% were eaten *in situ*, and 54.2% were removed. A similar hump-shaped pattern was detected between seeds size and the probability of seed removal (seed size, $z = 11.46$, $P < 0.001$; seed size^2, $z = -7.38$, $P < 0.001$; Fig. 1d). The proportion of seeds removed ranged from 6.7% to 100% among the 30 species. Five species showed a hump-shaped pattern, 9 species showed a positive trend, 1 species showed a U-shaped pattern, and 15 species showed no effect of seed size on the probability of seed removal (including 1 species with all the harvested seeds being removed) (Table 2).

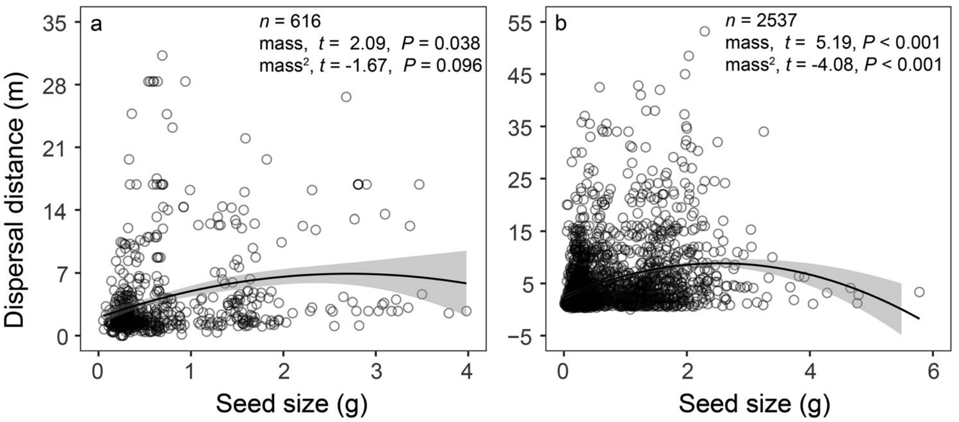

Figure 2 Effects of seed size on the dispersal distance. The regression lines with 95% confidence bands were based on the linear model.

Removal distance

Of the 3347 seeds removed in 2017, 18.4% were retrieved and the distances from their original releasing points were measured, with a range being from 0 to 31.25 m (mean ± SD: 3.99 ± 5.01 m). Removal distance generally increased with seed size until 2.5 g, above which removal distance declined slightly (linear mixed model, seed size, $t = 2.09$, $P = 0.038$; seed size^2, $t = -1.67$, $P = 0.096$; Fig. 2a). The mean removal distances ranged from 0.86 to 11.20 m among the 28 species. One species showed a U-shaped pattern, 1 species showed a positive effect and the remaining 26 species showed no effect of seed size on removal distance (including 9 species that were not statistically analyzed because of the small sample sizes) (Table 1).

Of the 5206 seeds removed in 2018, 48.7% were retrieved with the removal distances ranging from 0 to 53.20 m (4.83 ± 6.00 m), and a hump-shaped pattern was detected between seed size and removal distance (seed size, $t = 5.19$, $P < 0.001$; seed size^2, $t = -4.08$, $P < 0.001$; Fig. 2b). The mean removal distances ranged from 0.85 to 12.94 m among the 30 species. In total, only 1 species showed a similar hump-shaped pattern as the overall pattern across species, and the remaining 29 species showed no effect of seed size on removal distance (Table 2)

Seeds dispersed successfully versus eaten after removal

Of the 616 seeds retrieved in 2017, 85.1% were eaten, and 14.9% were successfully dispersed. A marginally significant relationship was detected between probability of seeds being successfully dispersed and seed size with the result that larger seeds were more likely to be dispersed rather than to be eaten after removal than smaller ones ($z = 1.77$, $P = 0.076$; Fig. 1e). The proportion of seeds dispersed differed among the 28 species, ranging from 0% to 100%. Two species showed a positive relationship between seed size and the probability of seeds dispersed, while the remaining 26 showed no clear seed size effect (including 12 species that were not statistically analyzed because of either the small sample sizes or most of the retrieved seeds were either successfully dispersed or eaten) (Table 1).

Of the 2537 seeds retrieved in 2018, 85.2% were eaten, and 14.8% were dispersed successfully. Larger seeds were more likely to be dispersed rather than eaten after being removed (Fig. 1f), although the model including the quadratic term of seed size was selected based on AIC (seed size, $z = 4.35$, $P < 0.001$; seed size^2, $z = -2.65$, $P = 0.008$). The proportion of seeds dispersed ranged from 0% to 100% among the 30 species. Finally, 1 species showed a positive effect of seed size on the probability of seeds being dispersed, 2 species showed a hump-shaped pattern and the remaining 27 showed no clear trends (including 7 species that were not statistically analyzed because most of the retrieved seeds were either successfully dispersed or eaten) (Table 2).

DISCUSSION

In this study, we found that seed size significantly affected all the processes of the rodent scatter-hoarding behavior across plant species, although most of the species showed no clear seed size effects on scatter-hoarding processes within species. Interestingly, seed size mediated the rodent foraging processes in different ways: a negative effect on the probability of seed harvest, a hump-shaped effect on the probability of seed removal and removal distance, while a positive effect on the probability of seeds dispersed successfully (i.e. the overwinter survival of cached seeds). Furthermore, these patterns of seed size effect were consistent between years.

Two opposite hypotheses have been proposed to explain the seed size effect on rodent foraging preference: (1) rodents prefer larger seeds as larger seeds hold more absolute energy (Gong *et al.* 2015; Wang *et al.* 2016); and (2) rodents reject larger seeds as larger seeds cost more handling time that may decrease foraging efficiency and increase foraging risks (Munoz & Bonal 2008; Jorge *et al.* 2012). Therefore, rodents may make a trade-off between the 2 opposite seed size effects and prefer to the medium-sized seeds (Wang *et al.* 2013; Dylewski *et al.* 2020). Our results proved that rodents made such balance within a single process of their foraging behavior (i.e. the hump-shaped pattern in seed removal process and removal distance). Moreover, our results also indicated that the tradeoff between selecting large versus small seeds also occurred between processes, that is the negative trend in seed harvest process (smaller seeds were more likely to be harvested which conformed to the second hypothesis) versus the positive trend in seed dispersal process (large seeds were more likely to be cached after being removed which conformed to the first hypothesis). The different seed size effects among scatter-hoarding processes found in this study may finally lead to a parabolic relationship between seed size and dispersal success, that is medium-sized seeds were more likely to be removed and cached, and to be transported with a further distance.

Plant seeds often show great variation not only in seed size but also in many other seed traits (e.g. nutrient contents, physical and chemical defenses) all of which play important role in seed dispersal and predation by rodents (Gong *et al.* 2015; Zhang *et al.* 2016; Wang *et al.* 2018). Current studies using multiple species of seeds often show different patterns of seed size effect on rodent foraging preference (Price 1983; Vander Wall 2003; Xiao *et al.* 2006b; Gong *et al.* 2015; Zhang *et al.* 2016). Different seed traits usually correlate with each other and co-influence the rodent foraging selection among species of seeds; it is therefore difficult to figure out which seed trait is the actual determinant of rodent foraging preference (Price 1983; Gong *et al.* 2015; Zhang *et al.* 2016). Our study provided a useful addition to this long-debated question. Despite the potential noisy effects of other seed traits, our results still showed a significant seed size effect on rodent foraging behavior in both years, indicating that seed size may be a vital factor in affecting rodent foraging preference among multiple species of seeds.

Our studied species differed greatly in the mean value (ranging from 0.06 to 4.84 g) and the range of seed size (from 0.12 to 9.60 g), and the multiple of the maximum and minimum seed size (ranging from 3-fold to 41-fold). Furthermore, the species also differ greatly in many other seed traits, including tannin, fat, protein, seed coat ratio, etc. (Gong *et al.* 2015, unpublished data). However, most of the species showed no clear effects of seed size within species, especially on seed harvest, seed removal distance and survival of cached seeds. There are several possible explanations: (1) the range of seed size within a single species may be not large enough to show a significant seed size effect; (2) for small-seeded species, rodents may have no interest in selecting among seeds because of the small amount of absolute nutrient content of any seed (Wang & Yang 2020); (3) while for large-seeded species, rodents may show no preference if the seeds are larger than a threshold (the segmented line model in Wang *et al.* 2013); (4) Seeds often contains diverse of chemical defense components (Kollmann *et al.* 1998; Vander Wall 2010), which may influence the effects of seed size; for example if a seed is rich in high toxic chemicals, rodents may reject it no matter it is big or small. (5) Seeds often show great interspecific variation in different nutrient contents, for example fat and protein (Xiao *et al.* 2006b; Gong *et al.* 2015), and the proportion of nutrient content of a seed may also bias the seed size effects (Wang & Yang 2014, 2015). Furthermore, the indirect seed–seed interaction (i.e. neighbor effect) is believed to affect rodent–seed interaction. For example, whether a given species of seeds would be ignored, eaten *in situ* or removed by rodents can be influenced by the existence of neighboring seeds (Ostoja *et al.* 2013). Different species of neighboring seeds often show different, even opposite patterns of neighbor effect (Garzon-Lopez *et al.* 2015; Yang *et al.* 2020), mainly because of the contrast of seed traits between the neighboring and focused seeds (Wang 2020b; Xiao *et al.* 2021). In our experiment, different species of seeds were randomly selected and released at a same point; therefore, for any given species of seeds that were distributed into several points, they may face different neighbor effects because of the different composition of species of seeds among points. Such variation of neighbor effect may dilute the effect of seed size on rodent foraging preference upon a specific species of seeds.

Current studies have often obtained different patterns of seed size effect on rodent scatter-hoarding behavior among forests, seasons and years, even using a same species of seeds, mainly because of the spatiotemporal variation in both seed and rodent abundance (Xiao *et al*. 2005; Wang *et al*. 2012; Chen *et al*. 2017). In our study, both rodent abundance (capture success: 6.5% in 2017 vs 12.2% in 2018) and seed production (unpublished seed rain data) in the forest differed between years. Several species did show different seed size effects between years. For example, *Amygdalus davidiana* showed a hump-shaped relationship between seed size and the probability of seed harvest in 2018 but not in 2017, while *Pinus armandii* showed a positive relationship between seed size and the probability of seed removal in 2017 but not in 2018 (Tables 1, 2). However, seed size showed a consistent effect across species in both years despite of the annual variation in either seed or rodent abundance, indicating that environmental factors may bias the results within single species, but not across species that hold a large range of seed size.

Individual plant species displayed diverse of patterns of seed size effects on rodent foraging preferences in both years: monotonic decrease and increase trends, hump-shaped and U-shaped patterns, although most species showed seed size-independent pattern, indicating that the effect of seed size is species specific. In conclusion, the effects of seed size on rodent foraging preference may be contingent on both intrinsic (e.g. other seed traits) and external (e.g. rodent abundance and seed availability) factors. The different seed size effects among species found in this study further suggest that a one-off study with only a few species might give misleading information on the overall pattern of seed size effect. However, the seed size effect across species was consistent in both years, indicating that including a large number of plant species that hold a sufficient range of the seed size may avoid the aforementioned bias to some extent. Future studies of effects of seed traits on animals' foraging preference should bear this in mind.

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REFERENCES

Blate GM, Peart DR, Leighton PM (1998). Post-dispersal predation on isolated seeds: A comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* **82**, 522–38.

Cao L, Wang Z, Yan C, Chen J, Guo C, Zhang Z (2016). Differential foraging preferences on seed size by rodents result in higher dispersal success of medium-sized seeds. *Ecology* **97**, 3070–8.

Chen Q, Tomlinson KW, 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**, 468–76.

Chen S, Wang B, Moles AT (2021). Exposure time is an important variable in quantifying post-dispersal seed removal. *Ecology Letter* **24**, 1522–5.

Dylewski L, Ortega YK, Bogdziewicz M, Pearson DE (2020). Seed size predicts global effects of small mammal seed predation on plant recruitment. *Ecology Letter* **23**, 1024–33.

Feng L, Chen S, Wang B (2021). Fine-scale spatiotemporal variation in seed–rodent interactions: A potential contribution to species coexistence. *Forest Ecology and Management* **498**, 119566.

Garzon-Lopez CX, Ballesteros-Mejia L, Ordonez A, Bohlman SA, Olff H, Jansen PA (2015). Indirect interactions among tropical tree species through shared rodent seed predators: A novel mechanism of tree species coexistence. *Ecology Letter* **18**, 752–60.

Gong H, Tang C, Wang B (2015). Post-dispersal seed predation and its relations with seed traits: A thirty-species-comparative study. *Plant Species Biology* **30**, 193–201.

Hirsch BT, Kays R, Pereira VE, Jansen PA, Rejmanek M (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letter* **15**, 1423–9.

Jansen PA, Bongers F, Hemerik L (2004). Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* **74**, 569–89.

Jorge MLSP, Brown JS, van der Merwe M (2012). Handling time and the evolution of caching behavior. *Behavioral Ecology* **23**, 410–7.

Kollmann J, Coomes DA, White SM (1998). Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Functional Ecology* **12**, 683–90.

Lai X, Guo C, Xiao ZS (2014). Trait-mediated seed predation, dispersal and survival among frugivore-dispersed plants in a fragmented subtropical forest, Southwest China. *Integrative Zoology* **9**, 246–54.

Li B, Hao ZQ, Bin Y, Zhang J, Wang M, Kühn I (2012). Seed rain dynamics reveals strong dispersal limitation, different reproductive strategies and responses to climate in a temperate forest in northeast China. *Journal of Vegetation Science* **23**, 271–9.

Lichti NI, Steele MA, Swihart RK (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Review* **92**, 474–504.

Moles AT, Warton DI, Westoby M (2003). Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* **84**, 3148–61.

Munoz A, Bonal R (2008). Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour* **76**, 709–15.

Ostoja SM, Schupp EW, Durham S, Klinger R (2013). Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. *Functional Ecology* **27**, 775–85.

Price MV (1983). Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* **60**, 259–63.

Sunyer P, Espelta JM, Bonal R, Muñoz A (2014). Seeding phenology influences wood mouse seed choices: The overlooked role of timing in the foraging decisions by seed-dispersing rodents. *Behavioral Ecology and Sociobiology* **68**, 1205–13.

Thein MM, Wu L, Corlett RT, Quan R, Wang B (2021). Changes in seed predation along a 2300-m elevational gradient on a tropical mountain in Myanmar: A standardized test with 32 non-native plant species. *Ecography* **44**, 602–11.

Thomson FJ, Moles AT, Auld TD, Kingsford RT (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* **99**, 1299–307.

Vander Wall SB (2003). Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* **100**, 25–34.

Vander Wall SB (2010). How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 989–97.

Wang B (2020a). Seed density affects post-dispersal seed predation: Evidence from a seed removal experiment of 62 species. *Integrative Zoology* **15**, 135–43.

Wang B (2020b). Neighbour effects do not always show consistent patterns, contrast of seed trait matters: Evidence from a seed-rodent mutualism study. *Behavioral Ecology and Sociobiology* **74**, 119.

Wang B, Chen J (2009). Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology* **90**, 3023–32.

Wang B, Ives AR (2017). Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. *Oecologia* **183**, 751–62.

Wang B, Phillips JS, Tomlinson KW (2018). Trade-off between physical and chemical defense in plant seeds is mediated by seed mass. *Oikos* **127**, 440–7.

Wang B, Wang G, Chen J (2012). Scatter-hoarding rodents use different foraging strategies for seeds from different plant species. *Plant Ecology* **213**, 1329–36.

Wang B, Yang X (2007). Seed predation of *Apodemus latronum* on 18 plant species in Northwest. *Zoological Research* **28**, 389–94.

Wang B, Yang X (2014). Teasing apart the effects of seed size and energy content on rodent scatter-hoarding behavior. *PLoS ONE* **9**, e111389.

Wang B, Yang X (2015). Seed removal by scatter-hoarding rodents: The effects of tannin and nutrient concentration. *Behavioural Processes* **113**, 94–8.

Wang B, Yang X (2020). Scatter-hoarding rodent foraging preference on nutrient content is mediated by seed size. *Current Zoology* **66**, 445–6.

Wang B, Ye C, Cannon CH, Chen J (2013). Dissecting the decision making process of scatter-hoarding rodents. *Oikos* **122**, 1027–34.

Wang Z, Zhang Y, Zhang D, Li J, Yi X (2016). Nutritional and defensive properties of Fagaceae nuts dispersed by animals: A multiple species study. *European Journal of Forest Research* **135**, 911–7.

Wrobel A, Zwolak R (2013). The choice of seed tracking method influenced fate of beech seeds dispersed by rodents. *Plant Ecology* **214**, 471–5.

Xiao Z, Zhang Z, Wang Y (2004). Impacts of scatter-hoarding rodents on restoration of oil tea *Camellia* *oleifera* in a fragmented forest. *Forest Ecology and Management* **196**, 405–12.

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

Xiao Z, Wang Y, Harris M, Zhang Z (2006b). Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest, Southwest China. *Forest Ecology and Management* **222**, 46–54.

Xiao Z, Zhang Z, Krebs CJ, Whitney K (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**, 1256–64.

Xiao Z, Zhang Z, Wang Y (2005). Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologica* **28**, 221–9.

Xiao Z, Holyoak M, Krebs CJ, Huang X (2021). Palatability and profitability of co-occurring seeds alter indirect interactions among rodent-dispersed trees. *Integrative Zoology* **00**, 1–11. https://doi.org/10.1111/1749-4877.12543

Yadok BG, Forget PM, Gerhard D, Aliyu B, Chapman H (2020). Seed nutrient content rather than size influences seed dispersal by scatterhoarding rodents in a West African montane forest. *Journal of Tropical Ecology* **36**, 174–81.

Yang X, Yan C, Gu H, Zhang Z (2020). Interspecific synchrony of seed rain shapes rodent-mediated indirect seed–seed interactions of sympatric tree species in a subtropical forest. *Ecology Letter* **23**, 45–54.

Zeng D, Jin T, Zhao Y, Yan C, Zhang Z, Ding P (2021). Rodent abundance triggered switch between the relative mutualism and predation in a rodent–seed system of the subtropical island forest. *Integrative Zoology* **16**, 109–19.

Zhang Z, Wang F (2001). Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Ecologica Sinica* **21**, 839–45.

Zhang Z, Wang Z, Chang G *et al*. (2016). Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. *Plant Ecology* **217**, 253–65.

Zhang Z, Yan C, Zhang H (2021). Mutualism between antagonists: Its ecological and evolutionary implications. *Integrative Zoology* **16**, 84–96.

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