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ORIGINAL ARTICLE

Differential seed mass selection on hoarding decisions among three sympatric rodents

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Abstract

Seed mass plays an important role in seed dispersal of many plant species during the hoarding process by rodents. Seeds of a particular plant species are usually dispersed by several sympatric rodent species. However, little is known about seed mass selection by different sympatric rodents that may show different hoarding behavior. In order to understand the role of different rodent species on the evolution of seed mass, we investigated the hoarding behavior and seed mass selection by three sympatric rodents (red spiny rat *Maxomys surifer*, Chinese white-bellied rat *Niviventer confucianus*, and yellow-bellied rat *Rattus flavipectus*) in semi-natural enclosures in southwest China. The hoarding behavior differed significantly among species: *M. surifer* showed predominantly scatter-hoarding behavior, *N. confucianus* showed both scatter- and larder-hoarding behavior, and *R. flavipectus* showed predominantly larder-hoarding behavior. All three rodent species preferred to remove and larder-hoard heavy seeds, but *M. surifer* and *R. flavipectus* were more selective on seed mass than *N. confucianus* during seed removal, while *R. flavipectus* were more selective than *M. surifer* and *N. confucianus* during larder-hoarding. The rodents showed contrasting preferences for seed mass during scatter-hoarding process. *M. surifer* and *N. confucianus* preferred to scatter-hoard heavy seeds, whereas *R. flavipectus* preferred to scatter-hoard light seeds. Our results show that different rodents may exert different selective pressures on seed mass during different dispersal processes. Changes in the composition of rodent communities, including those caused by human disturbance such as forest fragmentation, may influence the fates of seeds with different mass and the evolution of seed mass.

Significance statement

Seed mass plays an important role in seed dispersal of many plants by scatter-hoarding rodents. Previous studies usually focus on seed-mass selection by the whole rodent community while ignore the interspecific variation; and they often obtain inconsistent results. By using the semi-natural enclosure, we detected differences in hoarding behaviors among sympatric rodent species, and their different preferences on seed mass. These different preferences may exert different selective pressures on seed mass. Changes in the composition of rodent communities may influence the fates of seeds with different mass and the evolution of seed mass. We suggest that differences in hoarding behavior among sympatric rodent species should be considered in future field studies, as this will help us to better understand the role of the whole rodent community in the evolution of seed mass of forest trees that depend on dispersal by rodents.

Keywords Foraging preference · Larder-hoarding · Scatter-hoarding · Seed dispersal · Seed mass selection · Sympatric rodents

Introduction

Seed mass plays an important role in the seed dispersal of many plants, including those that depend on dispersal by scatter-hoarding rodents (Forget et al. 1998; Jansen et al. 2002, 2004). Seed mass can affect seed predation, removal, and caching by rodents (Wang and Chen 2009; Wang et al. 2013; Yi and Wang 2015), recovery of cached seeds by seed hoarders (Gomez 2004), and the dispersal fitness of seeds (Jansen et al. 2002; Cao et al. 2016). However,

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previous studies have obtained inconsistent results about the effects of seed mass on both rodent foraging behavior and seed survival during the scatter-hoarding processes. For example, some studies suggested that heavy seeds were more likely to be removed and scatter-hoarded, transported further away from parent trees (Forget et al. 1998; Jansen et al. 2002; Jansen et al. 2004; Vander Wall 2008), and more likely to germinate and survive (Jansen et al. 2004); while other studies found that seed mass showed little effect on the scatter-hoarding behavior of rodents (Brewer 2001; Xiao et al. 2004) or ultimate seed survival (Zhang et al. 2008). Furthermore, some studies found seeds with intermediate mass were more likely to be scatter-hoarded (Theimer 2003) and to establish as seedlings (Cao et al. 2016). These inconsistent findings suggest that the selection of seed mass by rodents during the scatter-hoarding processes is complicated and the mechanism remains unclear. In addition to scatter-hoarding, some rodent species also show larder-hoarding behavior, i.e., hoarding their seeds in a single or a few large caches (Hollander and Vander Wall 2004; Chang and Zhang 2014; Wang et al. 2014; Zhang et al. 2016). However, to our knowledge, no studies have targeted the effects of seed traits (especially seed mass) on the larder-hoarding behavior of rodents.

Seeds of a specific plant species are often dispersed by several sympatric rodent species, and the predation and hoarding behaviors may differ significantly among species (Hollander and Vander Wall 2004; Lu and Zhang 2008; Chang and Zhang 2014; Wang et al. 2014; Zhang et al. 2016). For example, Edward's long-tailed rats (*Leopoldamys edwardsi*) (Chang and Zhang 2011) and red spiny rats (*Maxomys surifer*) (Wang et al. 2014; Geng et al. 2017) showed predominantly scatter-hoarding behavior (i.e., caching of single seed in many different places, usually in the soil or litters), Chinese white-bellied rats (*Niviventer confucianus*) and chestnut rats (*Niviventer fulvescens*) showed both scatter- and larder-hoarding behavior (storage of many seeds together in a deep underground borrow, from which germination and establishment are unlikely) (Cao et al. 2011; Chang and Zhang 2011; Wang et al. 2014), and yellow-bellied rats (*Rattus flavipectus*) showed predominantly larder-hoarding behavior (Cao et al. 2011; Wang et al. 2014). Different rodent species also show different foraging preferences on seed mass (Munoz and Bonal 2008). A positive selection on seed mass would be expected if rodents prefer to scatter-hoard heavy seeds (Jansen et al. 2002, 2004) and a negative selection if rodents prefer to eat or larder-hoard heavy seeds (Gomez 2004; Cao et al. 2016). Different rodent community compositions may therefore lead to different preferences on seed mass during seed predation and dispersal processes. Therefore, in order to better understand the role of seed mass on seedling regeneration and the evolution of the seed mass, it is essential to consider the differences in seed mass preferences among sympatric rodent species. However, most previous studies focusing on seed mass selection by rodents in the forest ignored this interspecific variation in foraging preference on seed mass (Jansen et al. 2002; Xiao et al. 2004; Zhang et al. 2008; but see Munoz and Bonal 2008).

Comparing seed selection among coexisting species under field conditions is very difficult, so in this study, we investigated seed predation and seed hoarding by three sympatric rodent species in semi-natural enclosures in the Xishuangbanna tropical region of southwest China. We wanted to answer the following questions: (1) Did the three rodent species differ in hoarding behaviors (scatter-hoarding vs. larder-hoarding)? (2) Did they differ in seed mass preference during the foraging process? Furthermore, we also pointed out some potential roles of different rodent species in the evolution of seed mass of forest trees.

Materials and 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. The average annual rainfall is approximately 1500 mm, with 80% in the wet season (May–October) and 20% in the dry season (November–April) (Cao and Zhang 1997). Tropical montane evergreen broad-leaf forest and tropical rain forest are the predominant vegetation types in this region (Zhu 2006).

Three rodent species were selected as experimental animals. Red spiny rat (*Maxomys surifer*, body mass about 115 g) and Chinese white-bellied rat (*Niviventer confucianus*, 86 g) are the dominant rodent species in the tropical montane evergreen broad-leaf forests and tropical rain forests (Wu et al. 1996; Wang et al. 2014; Cao et al. 2016, 2017). Yellow-bellied rat (*Rattus flavipectus*, 127 g) is the dominant species in some fragmented forests (Chen 2017).

The seeds of *Castanopsis hystrix* were selected to study the predation and hoarding behavior of scatter-hoarding rodents because (1) *C. hystrix* is the dominant tree species in the tropical montane evergreen broad-leaf forest (Zhu 2006), and (2) all the rodent species in our study area preferred to predate and hoard *C. hystrix* seeds (Wang et al. 2014). The fresh seed mass varied from 0.24 to 2.75 g, with a mean of 0.93 ± 0.04 g (mean ± SE). The thickness of the seed coat is 0.34 ± 0.01 mm and the tannin content is about 0.15% (Wang et al. 2014). All the experimental seeds were collected from the forest during the fruiting time and then stored (mixed with dry sand) at 4 °C for later use.

Enclosure experiments

Rodents were captured by using live traps made of steel wire mesh (L × W × H = 14 cm × 14 cm × 30 cm) (Chang et al. 2009), baited with shelled peanuts and *Pittosporopsis kerrii* seeds. Species, body mass and reproductive status of captured individuals were recorded. Adults of our target species were taken back to the laboratory for enclosure experiments. Pregnant and juvenile individuals were released immediately. Before the enclosure experimental trails, all animals were kept in individual cages (40 cm × 30 cm × 25 cm) 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. Thirteen individuals (5 female, 8 male) of *M. surifer*, 12 individuals (5 female, 7 male) of *N. confucianus*, and 12 individuals (7 female, 5 male) of *R. flavipectus* were used in the experiments. To minimize observer bias, blinded methods were used when all behavioral data were recorded and analyzed.

Experiments were conducted in eight semi-natural enclosures (L × W × H = 10 m × 10 m × 1.5 m), which was located in Xishuangbanna Tropical Botanical Garden (see Wang et al. 2014 for details). During the experiments, only one rodent individual was placed in an enclosure for observation each time. Each animal was provided with commercial mouse chow and peanut on the first day to ease adaptation to the new environment. On the second day, 100 marked *C. hystrix* seeds were placed at the seed station (i.e., center of the enclosure) after being weighed individually. Seeds were marked by attaching a small coded plastic tag individually by a thin steel thread (Zhang and Wang 2001; Xiao et al. 2006). To ensure that each rodent was offered a full range of seed mass, the 100 seeds for each trial were divided into the following categories: less than 0.5 g ($n = 14$), between 0.5 and 0.7 g ($n = 14$), between 0.7 and 0.9 g ($n = 14$), between 0.9 and 1.1 g ($n = 14$), between 1.1 and 1.3 g ($n = 14$), between 1.3 and 1.5 g ($n = 14$), and heavier than 1.5 g ($n = 16$). Seeds were checked every day until most seeds were harvested by rodents. In this study, we were interested in the final seed fates and the different seed mass selection among rodent species; however, we also compared the seed mass preferences on each of the hierarchical choices of foraging processes among rodent species. At the end of our experiment, no seeds were left intact at the original seed releasing stations; thus the seed fates were first divided into two categories: eaten by rodents in situ and removed from original seed stations; and seed removal is usually treated as a parameter of seed dispersal as removed seeds have some potential of being successfully dispersed (Wang et al. 2013). Seeds removed were then determined to be either eaten after removal or hoarded by rodents, and hoarded seeds were determined to be scatter-hoarded (seeds removed away from the seed station, and buried by rodents under leaf litter or in the soil; each cache contained one or a few seeds, and most caches contained only one seed) or larder-hoarded (seeds carried into underground burrows that were more likely to be eventually eaten). In order to assess the effect of seed mass on seed survival, we divided the final seed fates into three categories: eaten by rodents (including seeds eaten both in situ and after removal), scatter-hoarded, and larder-hoarded. The experiment lasted 3–16 days for each individual. We did not check the seeds that were carried into the underground burrow until the end of the experiment to avoid disturbing the hoarding behavior of the rodents.

Data analysis

A generalized linear model (GLM) was used to analyze the differences in the probability of each seed fate among the three rodent species, using R version 3.4.1 (R Development Core Team 2017). Rodent species was treated as fixed variable and rodent individual as random variable. The sampling unit was the proportion of seeds removed, eaten, scatter-hoarded, or larder-hoarded by each rodent individual of all the released seeds, modeled as a binomial distribution with a logit-link function. Tukey's test (implemented through the *lsmeans* package) was used to do pair-wise comparisons between rodent species.

Effects of seed mass (as measured by fresh seed mass) on each seed fate was analyzed by generalized linear mixed models (GLMMs, in package *lme4*). The sampling unit is individual seed and seed fate was modeled as a binomial variable with a logit-link (1 for success and 0 for failure). Seed fresh mass was a continuous explanatory variable and rodent individual was treated as a random effect. Wald chi-square tests were performed to test the significance of fixed categorical variables in GLMMs using Anova function in *car* package. We performed model selection by comparing GLMMs with and without quadratic terms based on a chi-square test and lower Akaike information criterion (AIC) values, testing the possible nonlinear relationships between seed fates and seed mass. The model selection showed a clear linear relationship between seed fates and seed mass. We tested the interactions between seed mass and rodent species when analyzing effects of seed mass on seed fates. Tukey's test (implemented through the *lsmeans* package) was used to compare the seed mass effects on seed fates between rodent species by comparing the gradient (β_{mass}) of regression lines. For the statistical analysis of the hierarchical rodent foraging processes (i.e., eaten in situ vs. removed, eaten vs. hoarded after removal and scatter- vs. larder-hoarded), a subset (i.e., the target seed fate category) of the whole seeds were used. While during the final seed survival analysis, we

Fig. 1 The probability of seeds being removed from seed stations, eaten, scatter-hoarded, and larder-hoarded by the three species of rodents (black bars: *M. surifer*; light gray bars: *N. confucianus*; dark gray bars: *R. flavipectus*). Different letters indicate significant differences among rodents ($P < 0.05$)

used the whole data set, i.e., each of the seed fate was analyzed within all the released seeds.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

The hoarding behavior of three species of rodents

All released seeds were either eaten in situ (6.3 ± 2.9 to 19.8 ± 7.4%, mean ± SE) or removed (80.2 ± 7.4 to 93.7 ± 2.9%) from the seed stations by rodents at the end of the experiments (Fig. 1). *M. surifer* ate 39.4 ± 8.6%, scatter-hoarded 49.8 ± 7.2%, and larder-hoarded 10.8 ± 2.2% of the released seeds (Fig. 1); *N. confucianus* ate 23.1 ± 7.6%, scatter-hoarded 19.5 ± 6.2%, and larder-hoarded 57.4 ± 9.6% of the released seeds (Fig. 1); and *R. flavipectus* ate 14.7 ± 6.2%, scatter-hoarded 1.2 ± 0.6%, and larder-hoarded 84.2 ± 6.4% of the released seeds (Fig. 1).

Fig. 2 a–f Effects of seed mass on the probability of seeds being eaten in situ or removed from seed stations (all seeds released were included). The regression lines with 95% confidence bands (gray) were based on GLMMs. Black lines at the top and bottom of panels represent the distribution of fresh mass of seeds that were a success (1) and failure (0) respectively

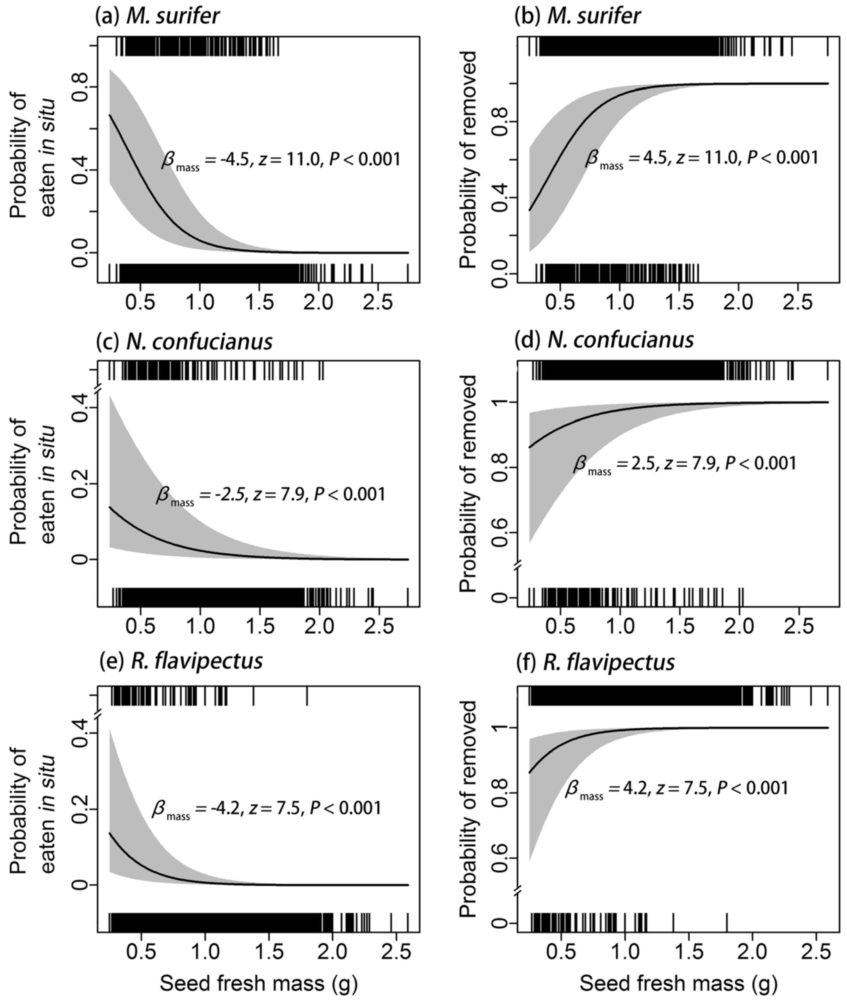

Table 1 Summary of Tukey's tests comparing the seed mass effects on seed fates between rodent species by comparing the gradient (β_{mass}) of regression lines in Fig. 2

	Removal		Eaten		Scatter hoarding		Larder hoarding	
Pair-wise between species	*z*	*P*	*z*	*P*	*z*	*P*	*z*	*P*
M. surifer and *N. confucianus*	4.0	< 0.001	1.6	0.265	− 1.6	0.260	0.7	0.788
M. surifer and *R. flavipectus*	0.4	0.496	3.0	0.007	3.6	0.001	− 6.1	< 0.001
N. confucianus and *R. flavipectus*	− 2.8	0.016	1.7	0.221	4.0	< 0.001	− 6.9	< 0.001

The probability of seeds being removed and larder-hoarded by *R. flavipectus* was much higher than *M. surifer* and *N. confucianus* (Tukey's test, all $P < 0.001$, Fig. 1). The probability of seeds being eaten and scatter-hoarded by *M. surifer* was significantly higher than *N. confucianus* and *R. flavipectus* (all $P < 0.001$, Fig. 1).

Effect of seed mass on the hierarchical choices of rodent foraging behavior processes

All the three rodent species preferred to remove heavy seeds away from seed station, while eat lightweight seeds in situ (GLMM, all $P < 0.001$; Fig. 2). *M. surifer* and *R. flavipectus* were more selective on seed mass than *N. confucianus* during seed removal (Table 1). Of the seeds removed, all rodent species prefer to hoard heavy seeds but eat lightweight ones (all $P < 0.001$; Fig. 3). While for the seeds hoarded, rodents showed different hoarding preferences upon seed mass among species. *N. confucianus* prefer to scatter-hoarded heavy seeds but larder-hoarded lightweight ones ($z = 3.8$, $P < 0.001$; Fig. 4c, d); however, *R. flavipectus* showed a distinctly opposite pattern, i.e., scatter-hoarding lightweight seeds but larder-hoarding heavy ones ($z = 3.3$, $P < 0.001$; Fig. 4e, f). While *M. surifer* showed no seed mass preference during either scatter- or larder-hoarding process ($P = 0.142$, Fig. 4a, b).

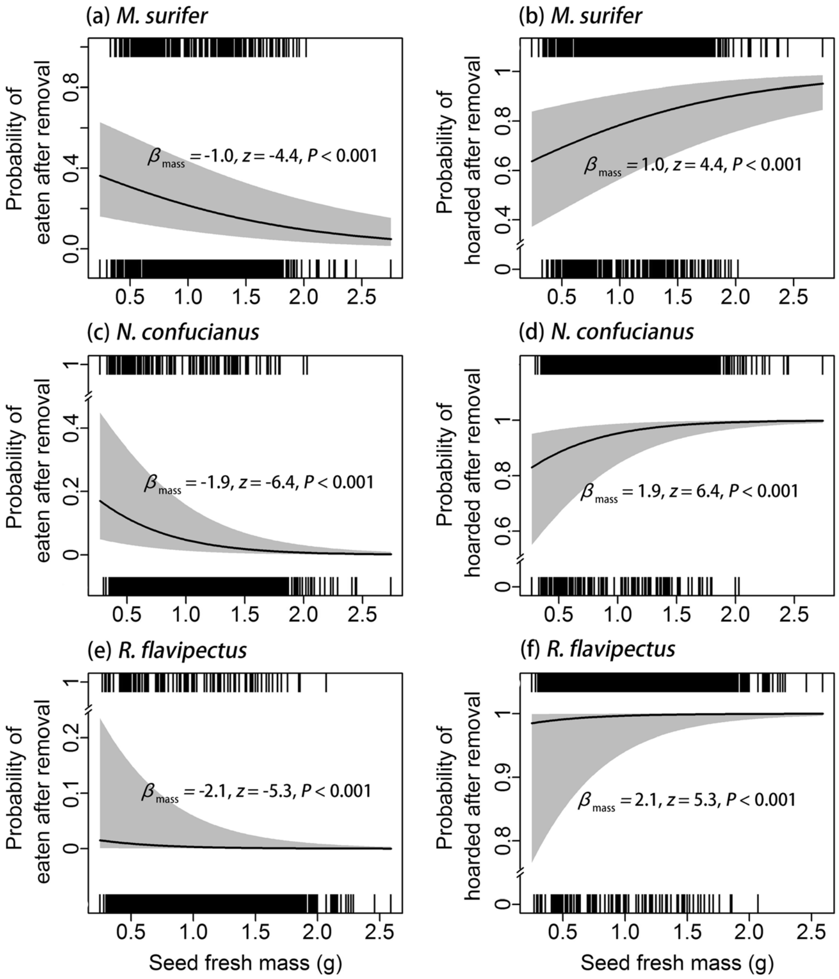

Fig. 3 **a–f** Effects of seed mass on the probability of seeds being eaten after removal or hoarded (only seeds removed were included). The regression lines with 95% confidence bands (gray) were based on GLMMs. Black lines at the top and bottom of panels represent the distribution of fresh mass of seeds that were a success (1) and failure (0) respectively

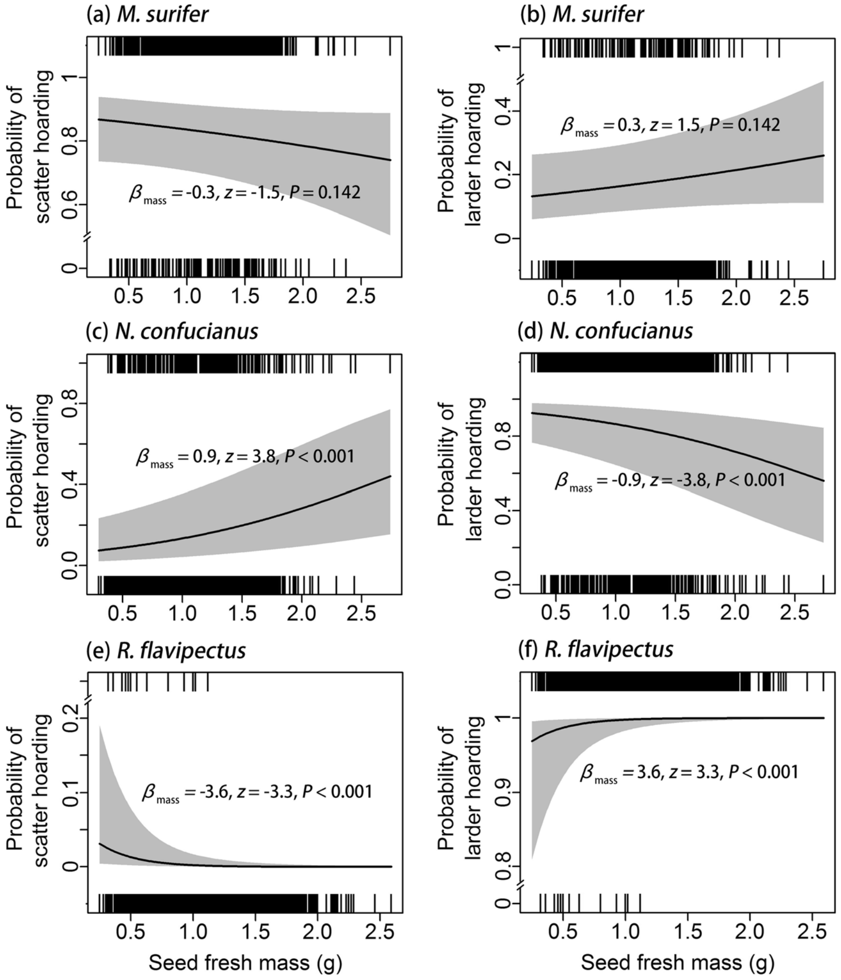

Fig. 4 **a–f** Effects of seed mass on the probability of seeds being scatter- or larder-hoarded (only seeds hoarded were included). The regression lines with 95% confidence bands (gray) were based on GLMMs. Black lines at the top and bottom of panels represent the distribution of fresh mass of seeds that were a success (1) and failure (0) respectively

Effect of seed mass on the final seed fate

Of all the released seeds, large seed mass increased the probability of seeds being larder-hoarded, but decreased the probability of seeds being eaten by all the three rodent species (GLMM, all $P <$ 0.001; Fig. 5). In contrast, the relationship between seed mass and scatter-hoarding varied greatly among rodent species. The probability of scatter-hoarding was positively related to seed mass in *M. surifer* ($\beta_{\text{seed mass}} = 1.0$, $z = 6.1$, $P < 0.001$; Fig. 5b) and *N. confucianus* ($\beta_{\text{seed mass}} = 1.4$, $z = 6.7$, $P < 0.001$; Fig. 5e), but was negatively related to seed mass in *R. flavipectus* ($\beta_{\text{seed mass}} = -2.0$, $z = -2.5$, $P = 0.014$; Fig. 5h).

Seed mass and rodent species showed an interactive effect on the probability of seeds being eaten ($\chi^2 = 9.5$, $P = 0.009$) and larder-hoarded ($\chi^2 = 49.7$, $P < 0.001$). Although all the rodent species preferred to lard-hoard heavy seeds and eat lightweight ones, *M. surifer* (Fig. 5a) was more selective on seed mass than *R. flavipectus* (the Tukey's test, $P = 0.007$; Table 1 and Fig. 5g) when eating seeds; while *R. flavipectus* (Fig. 5i) was more selective on seed mass than both *M. surifer* ($P < 0.001$; Table 1, Fig. 5c) and *N. confucianus* ($P < 0.001$; Table 1, Fig. 5f) during larder-hoarding.

Discussion

Our study showed that hoarding behavior differed significantly among the three species of rodents. *M. surifer* showed a predominantly scatter-hoarding behavior, *N. confucianus* showed both scatter- and larder-hoarding behaviors, and *R. flavipectus* showed a predominantly larder-hoarding behavior. The rodents that showed predominantly scatter-hoarding behavior are likely to enhance seed dispersal and seedling regeneration of trees; in contrast, the rodents that showed predominantly larder-hoarding behavior are likely to be detrimental to seed dispersal and seedling regeneration.

During the foraging processes, all the rodent species showed similar seed mass preference on each of the hierarchical choices except for the hoarding process, i.e., scatter- vs. larder-hoarded (Figs. 2, 3, and 4). However, our results from the final seed fate analysis showed that all the three species of rodents preferred to remove and to larder-hoard heavy seeds, while only *M. surifer* and *N. confucianus* preferred to scatter-hoard heavy seeds. Several studies also showed a similar preference for heavy seeds during seed removal and scatter-hoarding by rodents (Forget et al. 1998; Jansen et al. 2002,

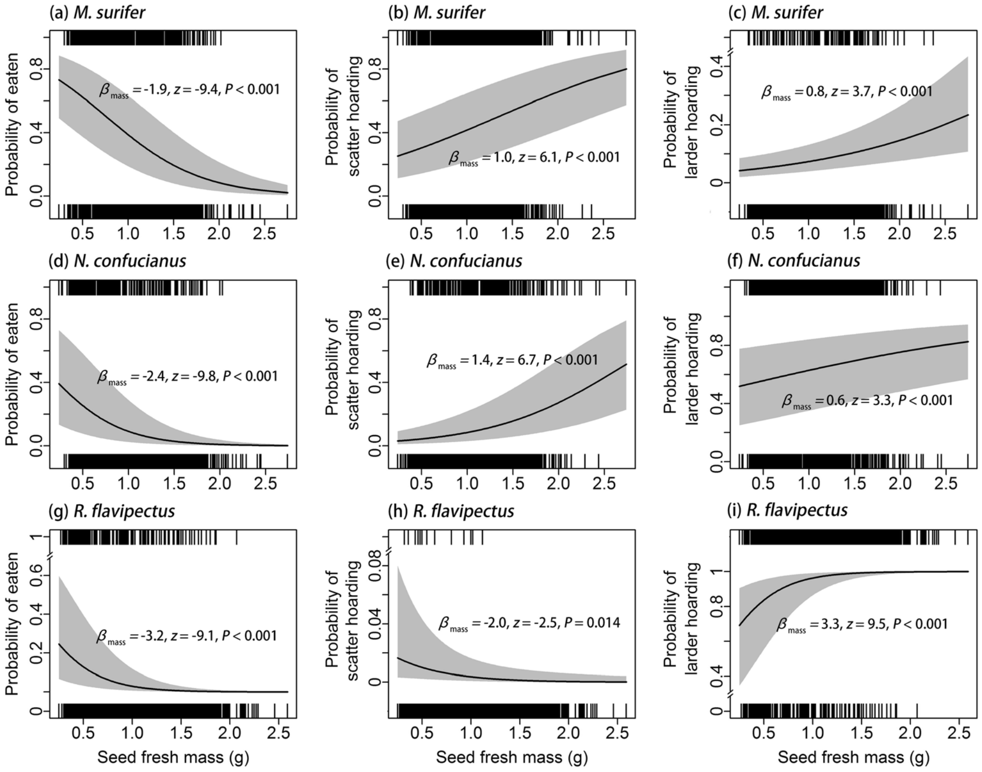

Fig. 5 **a–i** Effects of seed mass on the final seed fates: eaten (including seeds eaten both in situ and after removal), scatter-hoarded, and larder-hoarded by the three species of rodents. The regression lines with 95% confidence bands (gray) were based on GLMMs (all seeds released were included). Black lines at the top and bottom of panels represent the distribution of fresh mass of seeds that were a success (1) and failure (0) respectively

2004; Vander Wall 2008), even the body size of seed dispersers differed greatly (Wrobel and Zwolak 2017), presumably because heavy seeds could offer more nutritional rewards. In addition, eating heavy seeds under the parent tree may increase the predation risk for rodents, because heavy seeds require a longer handling time (Jacobs 1992). Larder-hoarding in the underground burrows could also reduce predation risk of rodents, as underground burrows are usually safer than either under the parent trees or under the shrubs where seeds were usually scatter-hoarded. Furthermore, larder-hoarding in deep burrows might be a strategy to reduce the pilferage of heavy seeds, because these are usually more likely to be pilfered after being scatter-hoarded (Gomez 2004).

Although all three species of rodents preferred to remove and larder-hoard heavy seeds, their selective pressures on seed mass varied greatly during the processes of seed removal and larder-hoarding (gradient of regression line varied greatly among rodent species, Table 1). *M. surifer* and *R. flavipectus* exerted a stronger positive selective pressure on seed mass than *N. confucianus* during seed removal, and *R. flavipectus* exerted a stronger negative selective pressure on seed mass than *M. surifer* and *N. confucianus* during larder-hoarding (since larder-hoarded seeds usually have high probability of being destroyed either by consumption or decay). Munoz and Bonal (2008) also found that selective pressures on seed mass varied between the Algerian mouse *Mus spretus* and the wood mouse *Apodemus sylvaticus* when they removed seeds, and they suggested that the reason might be the difference in the ratio of seed mass to rodent body mass (*M. spretus*, from 3.2 to 94.9%; *A. sylvaticus*, from 1.8 to 54.5%). However, the ratios of seed mass to rodent body mass in our study were much smaller than Munoz and Bonal (2008) observed, and were very similar among the three species (*M. surifer*, from 0.2 to 2.4%; *N. confucianus*, from 0.3 to 3.2%; *R. flavipectus*, from 0.2 to 2.2%).

The seed mass preference also differed significantly among rodents species when they scatter-hoarded seeds. *M. surifer* and *N. confucianus* preferred to scatter-hoard heavy seeds, whereas *R. flavipectus* preferred to scatter-hoard light seeds. As some scatter-hoarded seeds could usually escape from predation and establish a seedling, *M. surifer* and *N. confucianus* may exert a positive selective pressure on seed mass during scatter-hoarding, whereas *R. flavipectus* may exert a negative selective pressure on seed mass. Selection pressures on seed mass can therefore differ both among rodent species and among dispersal stages by the same species. The preference for removing and scatter-hoarding heavy seeds by *M. surifer* and *N. confucianus* may exert a positive selection pressure on seed mass, whereas the preference for larder-hoarding heavy seeds by *R. flavipectus* may exert a negative selection pressure.

Our results show that the hoarding behavior and foraging preference on seed mass during seed dispersal differed greatly among rodent species. Differential preferences on seed mass during scatter-hoarding by different rodents and conflicting selective pressures on seed mass at different dispersal stages may lead to inconsistent selective pressures on seed mass of a specific tree species. It is possible that selection by the whole rodent community may result in both positive and negative selection on seed mass in the same area, since the composition of the rodent community often varies greatly both among forests and among years (Wu et al. 1996; Wang et al. 2014; Cao et al. 2017; Chen 2017). This may explain, at least in part, the inconsistent results of previous studies that investigated seed mass selection by rodents during seed dispersal (Brewer 2001; Jansen et al. 2002, 2004; Theimer 2003; Xiao et al. 2004; Zhang et al. 2008; Cao et al. 2016).

Galetti et al. (2013) found that the extinction of large-gaped seed dispersers caused by fragmentation in the Brazilian Atlantic forest could reduce the seed dispersal of large seeds and result in a reduction in the seed size of a keystone palm species. In our study area, fragmentation is also a major threat to the local forests (Li et al. 2008; Liu and Slik 2014; Chen et al. 2017), which may also potentially reduce seed dispersal of heavy seeds. *R. flavipectus*, the dominant species in fragmented forests (Chen 2017), showed a predominantly larder-hoarding behavior and preferred to scatter-hoard light seeds, whereas *M. surifer* and *N. confucianus*, which preferred to scatter-hoard heavy seeds, were the dominant species in the continuous forests (Wu et al. 1996; Wang et al. 2014; Cao et al. 2016, 2017).

Our enclosure experiments could not examine the effect of seed mass on the ultimate seedling establishment, but they allowed the testing of specific hypotheses that are difficult to test under natural conditions. By using the semi-natural enclosure, we detected differences in hoarding behaviors among sympatric rodent species, and their different preferences for seed mass during their scatter-hoarding processes. These different preferences may exert different selective pressures on seed mass. We suggest that differences in hoarding behavior among sympatric rodent species should be considered in future field studies, as this will help us to better understand the role of the whole rodent community in the evolution of seed mass of forest trees that depend on dispersal by rodents.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval This study followed the ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching (ASAB/ABS 2012) and was approved by the committee on ethics of animal experiments of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (Permit Number: XTBG2014-002). After the experiments, all rodents were released at the site where they were captured.

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