Differential foraging preferences on seed size by rodents result in higher dispersal success of medium-sized seeds

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Abstract. Rodent preference for scatter-hoarding large seeds has been widely considered to favor the evolution of large seeds. Previous studies supporting this conclusion were primarily based on observations at earlier stages of seed dispersal, or on a limited sample of successfully established seedlings. Because seed dispersal comprises multiple dispersal stages, we hypothesized that differential foraging preference on seed size by animal dispersers at different dispersal stages would ultimately result in medium-sized seeds having the highest dispersal success rates. In this study, by tracking a large number of seeds for 5 yr, we investigated the effects of seed size on seed fates from seed removal to seedling establishment of a dominant plant *Pittosporopsis kerrii* (Icacinaceae) dispersed by scatter-hoarding rodents in tropical forest in southwest China. We found that small seeds had a lower survival rate at the early dispersal stage where more small seeds were predated at seed stations and after removal; large seeds had a lower survival rate at the late dispersal stage, more large seeds were recovered, predated after being cached, or larder-hoarded. Medium-sized seeds experienced the highest dispersal success. Our study suggests that differential foraging preferences by scatter-hoarding rodents at different stages of seed dispersal could result in conflicting selective pressures on seed size and higher dispersal success of medium-sized seeds.

Key words: larder-hoarding; scatter-hoarding; seed dispersal; seed dispersal success; seed size selection; seedling establishment; small rodents.

Introduction

The effect of seed size on seed fate under rodent predation has attracted a great deal of attention, but with conflicting findings (Forget et al. 1998, Brewer 2001, Jansen et al. 2002, 2004, Theimer 2003, Vander Wall 2003, Gomez 2004, Xiao et al. 2004, 2015, Zhang et al. 2008, Wang and Chen 2009, Lai et al. 2014). However, it is clear that seed size plays an important role in plant life history, in particular seed dispersal, seedling emergence, and seed survival (Janzen 1971, Venable and Brown 1988, Vander Wall 2010). Large seed size has often been viewed as an adaptation to many biotic and abiotic factors as large seeds could provide benefits in competition, shading, drought, herbivory, and nutrient limitation (reviewed in Leishman et al. 2000). Consequently, directional phenotypic selection favoring large seed size has been widely accepted (Leishman et al. 2000, Vander Wall 2001). In addition, preference for large seeds by scatter-hoarding animals (e.g., rodents) during the dispersal stage would also favor the evolution of large seeds (Smith and Reichman 1984, Vander Wall 2001, 2003,

2010, Jansen et al. 2002, 2004). However, conclusions drawn from these studies were primarily based on observations at earlier stages of seed dispersal (seed removal and caching), or based on a limited sample size of established seedlings.

Recent studies indicated that large seeds could be at a disadvantage for survival after seed removal because they have a stronger odor and are more likely to be pilfered by rodents (Gomez 2004). Seed size may also impose a trade-off between the total number of offspring and individual propagule size such that Smith and Fretwell (1974) suggested that there is an optimal propagule size for an organism to maximize the fitness of the mother. Some studies indicated that plants show a trade-off between seed size and offspring numbers to maximize the fitness of the plants (Venable 1992, Eriksson and Jakobsson 1999, Turnbull et al. 1999, Brancalion and Rodrigues 2014). However, it is not clear if there is a trade-off during the dispersal process and what implications that would have for plant seed size.

Seed dispersal, from seed removal to seedling establishment, is a complex process involving several stages. It can logically be classified into pre-removal, post-removal stage, and seedling establishment. The effects of seed size on dispersal success can be inconsistent across different

dispersal stages (Jansen 2003, Gomez 2004, Munoz and Bonal 2008, Zhang et al. 2008), leading to conflicting selective pressures.

Recently, some studies suggested that large seeds have higher dispersal success (Jansen et al. 2002), because large seeds are more likely to be removed and scatter-hoarded (Forget et al. 1998, Jansen et al. 2004, Vander Wall 2008, Xiao et al. 2015) and tend to be cached further away from parent trees, as well as in lower densities (Jansen et al. 2002, 2004, Xiao et al. 2004); thus, they are more likely to establish as seedlings (Jansen et al. 2004). However, some studies found that seed size did not significantly affect the scatter-hoarding behavior of small rodents (Brewer 2001, Xiao et al. 2004), or that small rodents preferred to scatter-hoard intermediate-sized seeds (Theimer 2003). Furthermore, some studies found that larger seeds have lower fitness during dispersal (Gomez 2004). This is because large seeds are more frequently recovered or pilfered after being cached, and suffer higher post-dispersal predation pressure than smaller seeds (Brewer 2001, Gomez 2004, Zhang et al. 2008). Differential rodent foraging preferences on seed size during different dispersal stages make it difficult to accurately assess the effects of seed size on dispersal success, because seed size selective pressure acting at a given stage can be altered or even offset by an opposite effect at another stage (Gomez 2004, Zhang et al. 2008). Consequently, it is necessary to investigate the effects of seed size on fitness during the whole dispersal period.

Here, we propose a conceptual model to predict the dispersal success of seeds based on their size (Fig. 1) in order to further understand how seed size affect seed fate at each stage, and subsequent dispersal success. We divided the dispersal process into two stages: stage 1, pre-removal (at seed station or under parent tree); stage 2, post-removal (removed from seed station or from parent tree). Seed dispersal success was defined as post-dispersal seedling establishment (Schupp et al. 2010). We assumed that, at stage 1, pre-removal seed survival was positively associated with seed size, as was shown in many previous studies (Jansen et al. 2002, 2004, Jansen 2003, Xiao et al. 2004, 2005, Zhang et al. 2008). At stage 2, post-removal seed survival would be negatively associated with seed size as suggested by Gomez (2004) and Zhang et al. (2008). Fig. 1a shows the association between seed survival and seed size is linear, where Fig. 1b shows the association between seed survival and seed size is nonlinear. Here, S_1 is the survival rate at stage 1 (pre-removal), S_2 is the survival rate at stage 2 (post-removal), S_0 is dispersal success. Then, $S_0 = S_1 S_2$. As such, the dispersal success takes on the form of a negative parabola, where medium-sized seeds have the highest dispersal success.

In this study, we investigated the effects of seed size (measured as seed mass) on the seed fate of *Pittosporopsis kerrii* Craib (Icacinaceae) from seed release to seedling establishment in the Xishuangbanna tropical forest, Yunnan, southwest China over a five-year period. We aimed to test two hypotheses: (1) large-sized seeds would
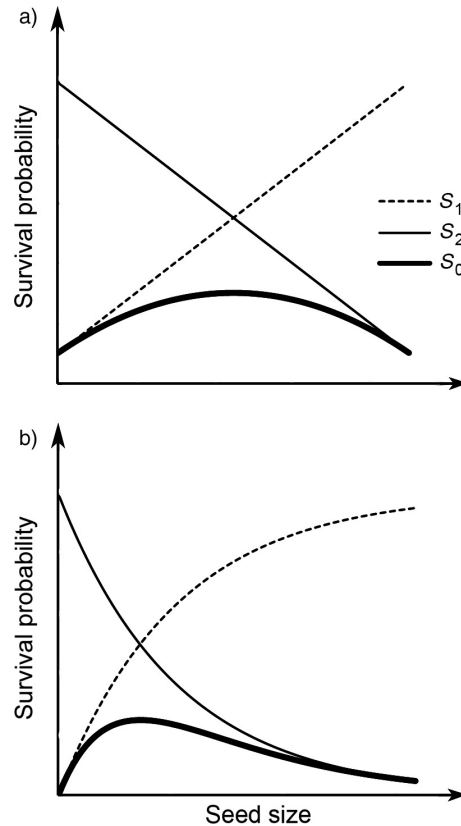
Fig. 1. Conceptual models for showing the relationship between seed size and the dispersal success (S_0) or seed survival at the (a) early (before removal, S_1) and (b) late (after removal, S_2) dispersal stages as predicted by the conflicting selective pressure hypothesis. $S_0 = S_1 S_2$.

have highest dispersal success because small-sized seeds are more likely predated while large-sized seeds are more likely dispersed; (2) due to differential rodent foraging preferences on seed size across different seed dispersal stages, medium-sized seeds would have the highest dispersal success as demonstrated in Fig. 1.

MATERIALS AND METHODS

Study site and species

This study was conducted in tropical forest located within the Menglun Nature Reserve, Xishuangbanna, Yunnan Province, China. The average annual rainfall is approximately 1,500 mm, with 80% in the wet season (May–October) and 20% in the dry season (November–April; Cao and Zhang 1997). The average annual temperature is 22°C. We selected three stands for presenting and tracking tagged seeds of *P. kerrii*. Stand 1 was a tropical montane evergreen broad-leaved forest, and was dominated by *Castanopsis echidnocarpa*, *Aporusa yunnanensis*, *Olea rosea*, *Lithocarpus truncates*, and *Schima wallichii* (Zhang and Cao 1995). Stand 2 was a tropical seasonal

rainforest, and was dominated by *Pometia tomentosa*, *Terminalia myriocarpa*, *Baccaurea ramiflora*, *Garcinia cowa*, *Alphonsea mollis*, and *Pseudouvaria indochinensis* (Zhang and Cao 1995). Both of these stands are located near a permanent plot of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (21°50′ N,101°12′ E, elevation 760 m). Stand 3 was a secondary forest (30 yr after prohibition of cultivation) located within the Xishuangbanna Tropical Botanical Garden (21°56′ N, 101°15′ E, elevation 550 m), and was dominated by *Gnetum montanum*, *Litsea glutinouse*, *Castanopsis indica*, *Phoebe lanceolata*, and *Schefflera venulosa* (Liu et al. 2014).

Pittosporopsis kerrii is a dominant shrub or small tree species in the tropical rainforest of the Xishuangbanna region (Lan et al. 2008). It is commonly seen in the tropical, montane, evergreen, broad-leaved forest. *P. kerrii* is very abundant in stand 2 and 3, and is commonly seen but less abundant in stand 1. The fruit of *P. kerrii* is a drupe, with a dry pericarp, suggesting that it evolved under dispersal by frugivorous animals, similar to almonds (Vander Wall 2001, Li and Zhang 2007). The fruit of *P. kerrii* become mature in August, and fall to the ground when they become ripe. The pericarp dehisces or becomes rotten quickly after the fruit falls to the ground. No seed was observed to be infested by insects. Small rodents strip the pulp away from the seeds and discard it while eating or hoarding the seeds. The fruit mass of *P. kerrii* is 7.14 ± 1.65 g (mean ± SD; $n = 98$); the fresh seed mass is 5.58 ± 1.40 g, ranging from <1.5 g to more than 13 g. The nutritional component of germinated seeds gradually transforms into a dormant taproot (within about 2–3 months; Cao et al. 2011*b*). This is the first seedling phase of *P. kerrii* and it is indigestible to rodents. Taproots develop into normal seedlings within several months, such that the appearance of taproots indicates that the *P. kerrii* seeds have successfully escaped predation by rodents.

In the study sites, *Niviventer confucianus* (body mass 86 g) is the most abundant rodent species and comprised 66.9% of captures (Wang et al. 2014). *Maxomys surifer* (11% of captures, body mass 115 g)*, Niviventer fulvescens* (12.5% of captures, body mass 69 g) and *Rattus flavipectus* (6.6% of captures, body mass 127 g) were also commonly seen within the experimental stands (Cao et al. 2011*a*, *b*, Wang et al. 2014). Several tree squirrel species (*Dremomys rufigenis*, *Callosciurus erythraeus*, and *Tamiops swinhoei*) were observed in the forest, but they were not abundant. Our trap experiment showed that *Niviventer confucianus* was the only abundant species in stand 1 (Appendix S1: Table S1), *N. confucianus* and *M. surifer* were the abundant species in stand 2, while *N. confucianus, N. fulvescens* and *M. surifer* were the abundant species in stand 3.

Seed releasing and tracking experiments

We selected three stands in the study area for releasing and tracking tagged seeds of *P. kerrii* from August 2007 to August 2011. During this period, we weighed 8,460 seeds and released them into the three stands (540 seeds per stand per year, except for 2007 when 900 seeds were released in stand 3). In each study stand, 18 (or 30 in stand 3 in 2007) seed stations were spaced 10–20 m apart along a single transect. At each station, 30 individually tagged seeds were placed on the surface of the ground. The tagged seeds at each seed station were covered using a steel wire-mesh enclosure (0.7 × 0.7 × 0.5 m, mesh size 1 × 1 cm), with one small hole (10 × 10 cm) on each side of the four walls to allow access by small rodents but prevent the entrance of large vertebrates, e.g., wild boar *Sus scrofa*. 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). Plastic tags have a negligible effect on seed removal (Xiao et al. 2006). The fates of the tagged seeds were surveyed at weeks 2, 4, 8, 12, 16, and 20 of the current year, and then in March, July, September, and December of the following year. Seeds at each station were categorized as intact, predated, or removed, and those removed from seed stations were categorized as scatter-hoarded (seeds buried in the surface soil or beneath leaf litters), larder-hoarded (seeds hoarded in underground burrows or tree cavities that were not favorable for seedling establishment and were eaten in the end), predated, missing (not located due to vision barrier or likely larder-hoarded in burrows), or established seedlings. In this study, the dispersal success was defined as seeds surviving to the seedling stage. Very few seeds were dispersed farther than 30 m (see *Results*). Missing seeds were excluded from analysis. We also recorded the dispersal distances of cached seeds from the source seed station. Cached seeds were marked using a numbered bamboo stick so they could be relocated. At subsequent visits, we checked the cached seeds until they were recovered (eaten or removed) by animals. If a marked cache was removed, the area around the cache was extensively searched in an attempt to relocate the seeds. When seeds in primary caches or higher-order caches (e.g., secondary caches, hoarded after primary caching) were removed and found in other caching sites, we also recorded the seed fate and distance. During each survey, we intensively searched the area within a 40 m radius around each seed station to retrieve the removed seeds and record seed fates. When we found some seeds were dispersed more than 30 m at one seed station, the search radius was increased to 50–60 m until we could not retrieve seeds within this area. We found 97.8% ($n = 4,177$) of seeds and seed fragments distributed within 30 m of seed stations in the primary dispersal stage; 97.4% ($n = 4,156$) of seeds and seed fragments were distributed within 30 m for the ultimate dispersal stage (including multiple movements); only 2.2% ($n = 92$) and 2.6% ($n = 113$) seeds were farther than 30 m for initial and ultimate dispersal distance, respectively. We spent 1–4 d (depending on the number of removed seeds) to search for the removed seeds in one stand for each survey. Three people searched for the removed seeds, and all three people searched the whole searching radius independently, but concurrently, for each survey.

Data analysis

Effects of seed size (as measured by fresh seed mass) on various seed fates were analyzed by generalized linear mixed models (GLMMs) in the lme4 package in R using linear and quadratic terms of seed size (R, version 3.2.5; R Development Core Team 2016). Seed fate modeled as a binomial variable with a logit-link (1 for success and 0 for failure). Seed fresh mass was a continuous explanatory variable with linear and quadratic terms; stand, year, and seed station were random effects structured as seed station nested within year and year nested within stand (confidence intervals of random effects see Appendix S2: Table S2). We then performed model selection by comparing GLMMs with and without quadratic terms based on chi-square test and lower Akaike information criterion (AIC) values, testing possible nonlinear relationship between seed fates and seed size. The model selections showed that seed fate at a seed station (seed removal and predation), fate after removal (predated and scatter-hoarded), ultimate fate (predated, established, or missing) during dispersal were best explained by the models with both linear and quadratic terms of seed mass, while the probability of larder-hoarded seeds and subsequent fates of scatter-hoarded seeds (recovered from caches or remaining in caches) were best explained by models with only a linear term of seed mass (Appendix S2: Table S1). Effect of seed size on the dispersal distance ($\log_{10}$-transformed to meet normal distribution assumptions of the statistical models) of cached seeds was similarly analyzed using linear mixed models (LMMs) considering linear and quadratic terms.

To test the effects of searching distance on our results, we presented the kernel density of ultimate dispersal distance for seeds larger and smaller than 6.5 g (seeds weighing about 6.5 g showed highest survival and seedling establishment, see *Results*) by using kernel density estimation through the ks package in R. If more large-sized seeds were dispersed beyond the searching distance, their density against dispersal distance distribution should have a larger and longer right tail. If their density against dispersal distance distribution was similar, the impact of searching distance on survival estimation of large- and small-sized seeds was minor.

<center>RESULTS</center>

Seed fate of the released seeds

We found 12.3% of seeds ($n = 1,044$) were not harvested by rodents (Fig. 2), and 57.1% ($n = 596$) of them germinated and established taproots at seed stations. Finally, 75% ($n = 447$) of the 596 taproots developed into seedlings at the seed stations.

Rodents removed 81.43% seeds ($n = 6,889$) from seed stations. Of the 6,889 removed seeds, 25.3% ($n = 1,745$) were scatter-hoarded. Finally, 347 seeds (5.0%) survived

to the stage of taproot establishment (Fig. 2). Of these taproots, 84% ($n = 293$) developed into seedlings.

Effect of seed size on pre- and post-removal seed fate

Analysis of the effects of seed size on the pre-removal fate showed that the probability of seed removal increased nonlinearly with seed mass (seed mass, $z = 10.7$, $P < 0.0001$; seed mass^2, $z = -7.2$, $P < 0.0001$; Fig. 3a). After seeds were removed from seed stations, there was a significant bell-shaped association between the probability of scatter-hoarded seeds and seed mass (seed mass, $z = 4.2$, $P < 0.0001$; seed mass^2, $z = -3.6$, $P = 0.0003$; Fig. 3b). Medium-sized seeds weighing about 6.5 g experienced a higher probability of scatter-hoarding than did small- or large-sized seeds. There was a marginal positive and significant association between the probability of larder-hoarded seeds and seed mass ($z = 1.8$, $P = 0.0773$; Appendix S2: Fig. S1).

Analysis of the effects of seed size on the ultimate fate of harvested seeds showed that there was a significant bell-shaped association between seed mass and the probability of seedling establishment (seed fresh mass, $z = 4.4$, $P < 0.0001$; seed fresh mass^2, $z = -3.8$, $P = 0.0001$; Fig. 3c), where medium-sized seeds (~6.5 g) had the highest success rates. Results based on separate analysis for three different stands were similar. There were significant bell-shaped associations between seed mass and the probability of seedling establishment in stand 1 and 3 (stand 1, seed fresh mass, $z = 3.0$, $P = 0.0026$; seed fresh mass^2, $z = -2.6$, $P = 0.0094$, Appendix S2: Fig. S2a; stand 3, seed fresh mass, $z = 2.6$, $P = 0.0097$; seed fresh mass^2, $z = -2.1$, $P = 0.0367$, Appendix S2: Fig. S2c), while there was a marginal significant bell-shaped association between seed mass and the probability of seedling establishment in stand 2 (seed fresh mass, $z = 2.0$, $P = 0.05$; seed fresh mass^2, $z = -1.9$, $P = 0.0592$, Appendix S2: Fig. S2b).

Dispersal distance

We found the majority of seeds (>97%) of the two seed groups (larger and smaller than 6.5 g) were dispersed within 30 m. The densities of ultimate dispersal distance of the two seed groups were similar (Fig. 4b). Results showed that the dispersal distance of cached seeds varied from 0.3 to 105 m with a mean of 8.1 m. We found there was a significant bell-shaped association between seed mass and dispersal distance (seed fresh mass, $t = 4.8$, $P < 0.0001$; seed fresh mass^2, $t = -3.3$, $P = 0.001$, Fig. 4a), where seeds that weighing about 8 g were dispersed further.

<center>DISCUSSION</center>

In this study, we found more small-sized seeds were predated while large-sized seeds were typically removed. However, after seed removal, large-sized seeds suffered a
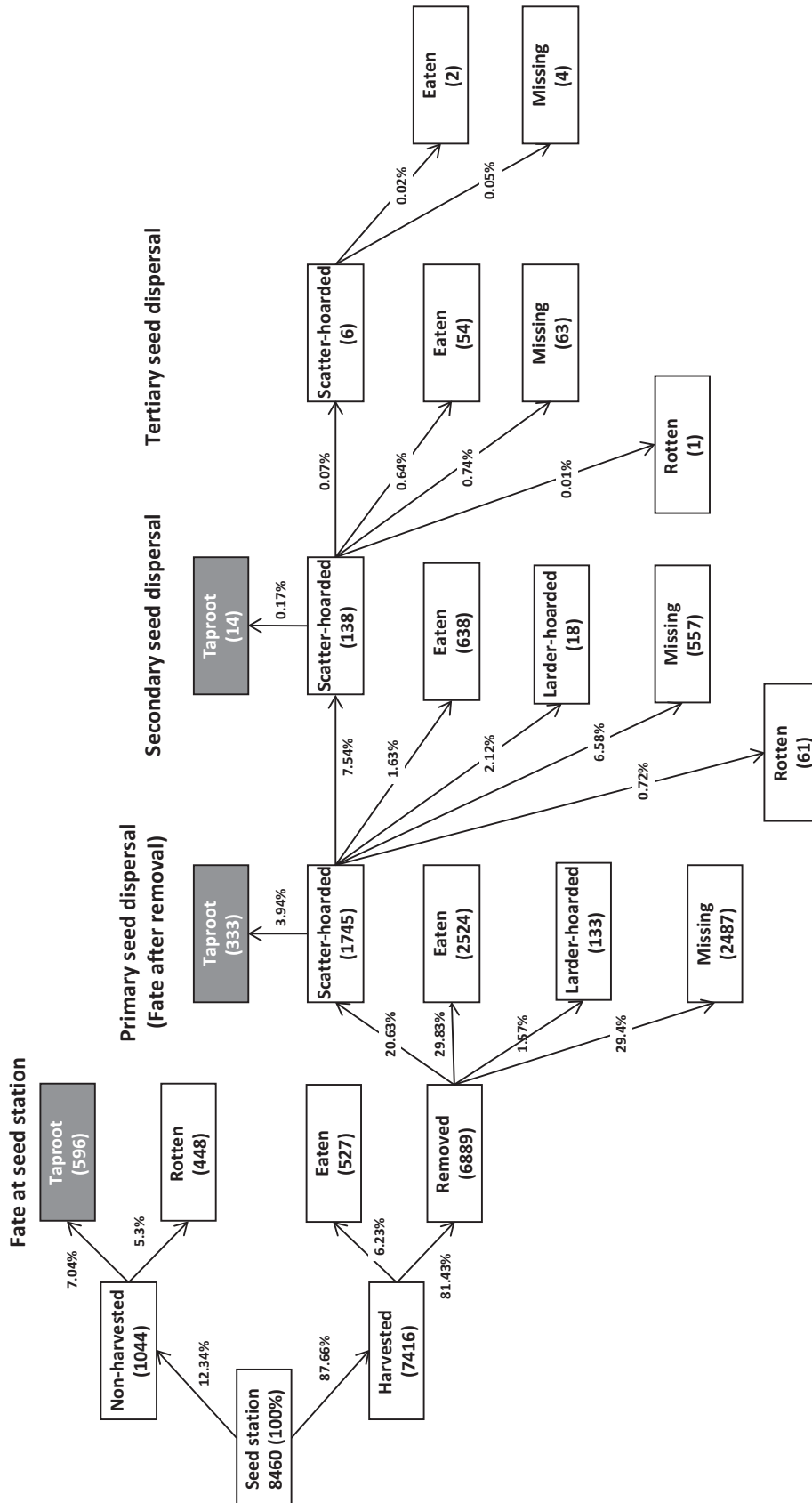
Fig. 2. Seed fate pathways of the 8,460 tagged seeds of *Pittosporopsis kerrii* after seed placement at seed stations.
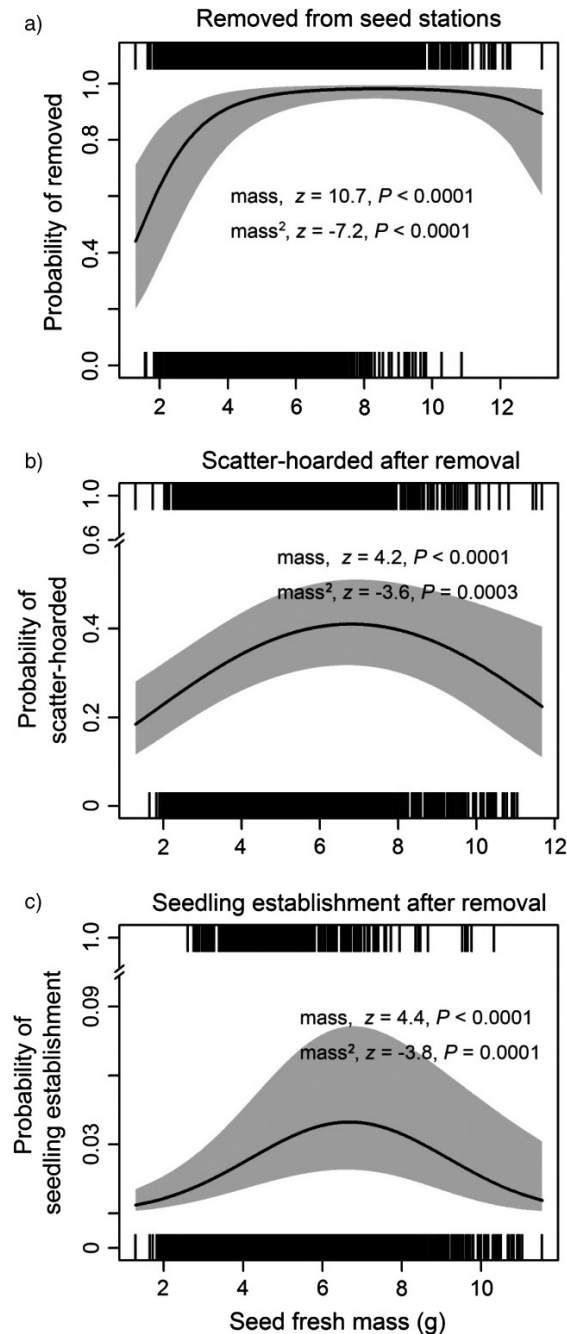
FIG. 3. Effects of seed mass on the probability of seeds (a) being removed from seed stations, (b) being scatter-hoarded after removal, and (c) seedling established after removal. The regression lines with 95% confidence bands (gray) were based on best-fitting models after model selection. Black lines at the top and bottom of panels represent the distribution of fresh mass of seeds that were success (1) and failure (0) respectively.

survival disadvantage and tended to be eaten or recovered after being cached (Appendix S2: Fig. S3). These observations suggest that differential rodent foraging preferences on seed size at different seed-dispersal stages will make medium-sized seeds have a higher dispersal success than

large- or small-sized seeds. The associations between seed size with pre- and post-removal seed survival rate were found to be nonlinear, supporting the prediction of Fig. 1b. Our results suggest that natural selection on seed size of plants under rodent predation and dispersal is more complicated than previously thought. Specifically, rodent foraging preferences exert conflicting selective pressure on seed size at different parts of the seed life stage.

Our results showed that medium-sized seeds experience higher probability of scatter-hoarding than small- and large-sized seeds. Previous studies have proposed that there should be a trade-off that animals must make in scatter-hoarding seeds of different sizes (Munoz and Bonal 2008, Tamura and Hayashi 2008, Wang et al. 2013, Lichti et al. 2015). Animals negotiate a trade-off between higher nutrient contents from larger seeds and higher costs of handling and transporting larger seeds (Theimer 2003, Munoz and Bonal 2008, Wang et al. 2013, Lichti et al. 2015). Some studies also found smaller-bodied rodents prefer to scatter-hoard small-sized seeds and larger-bodied rodents prefer to scatter-hoard large-sized seeds (Tamura and Hayashi 2008). Gomez (2004) reported that large seeds were more likely to be pilfered after being cached. This may be because large seeds may attract more attention when being cached as they contain more nutritional value, and were more likely to be pilfered. Similar to our findings, Zhang et al. (2008) found large-sized seeds were more likely to be recovered or pilfered after being cached. Thus, the high pilferage of large-sized seeds can be attributed to the observed lower scatter-hoarding of large-sized seeds.

Apart from high pilferage of large-sized seeds, large-sized seeds were more likely to be eaten after removal, suggesting that the higher dispersal success of large-sized seeds in the early stage was offset in later stages by both higher pilferage and eating rates. We also found large seeds were more likely to be larder-hoarded and two rodent species (*M. surifer* and *R. flavipectus*) preferred to larder-hoard large-sized seeds (Cao Lin et al., *unpublished data*). Because the larder-hoarding of seeds does not contribute to seeding establishment, rodent preference for larder-hoarding large-sized seeds will reduce dispersal success of large seeds. As the dispersal distance of most seeds was found to be smaller than our searching distance (Fig. 4), the missing seeds in field experiments were thought to be transported into underground burrows or tree cavities, as observed in many previous studies (Vander Wall 1990, Clarke and Kramer 1994, Steele et al. 2001, Hollander and Vander Wall 2004, Moore et al. 2007, Somanathan et al. 2007, Lu and Zhang 2008, Steele 2008, Chang et al. 2010, Chang and Zhang 2011, Huang et al. 2011). Recent studies also indicated that some rodents preferred to larder-hoard large seeds in underground burrows (Chang et al. 2010, Wang et al. 2014). These results indicate that the conventional view, based on the observation of the early dispersal stage of seeds, may not be adequate in explaining dispersal success in some species or ecosystems if seed size does not confer

a)
Dispersal distance of cached seeds

mass, $t = 4.8$, $P < 0.0001$

mass^2, $t = -3.3$, $P = 0.001$

b)
Distribution of ultimate dispersal distance
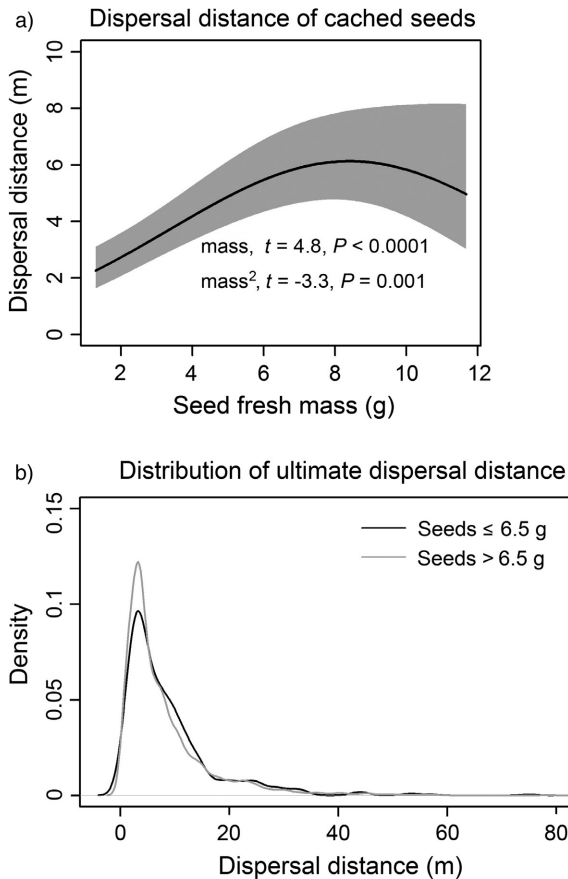

Seeds ≤ 6.5 g
Seeds > 6.5 g

FIG. 4. Effects of seed mass on (a) the dispersal distance of cached seeds and (b) estimated kernel density of ultimate dispersal distance for two-group seeds larger or smaller than 6.5 g (including cached seeds and seed fragments). The regression line with 95% confidence bands (gray area) in Fig. 4a were based on best-fitting models after model selection.

consistent advantages or disadvantages across dispersal stages.

There is a possibility that seeds were transported to places out of the searching range (see Jansen et al. 2004, 2012). The missing seeds outside of the search area likely caused a biased estimate in our study, if the majority of seeds outside of the searching area were skewed toward one size class. Analysis of association between seed mass and missing seeds showed that medium-sized seeds weighing about 8 g were more likely to be missing than large- or small-sized seeds (Appendix S2: Fig. S4), suggesting that the probability of seedling establishment for medium-sized seeds may be underestimated if some of the missing seeds were transported outside of the search area and escaped predation and established seedlings. One driver of missingness could be seed dispersal outside the searching area. However, the density of ultimate dispersal distance distribution for large- and small-sized seeds demonstrated no obvious differences in their right tails (Fig. 4b), suggesting the difference between large- and small-sized seeds in number of seeds

dispersed beyond the searching distance was minor. Furthermore, Fig. 4b indicated that number of seeds with dispersal distance larger than 20 m (much smaller than our searching distance of 40 m) decreased very rapidly. Thus, the impact of searching distance on survival estimation of large- and small-sized seeds can be ignored. This was probably because the body mass of the rodents in our study was relatively small, and the dispersal distance was much smaller than our searching distance.

We found medium-size seeds have the highest dispersal success for harvested seeds. This trend was consistent when seedlings of non-harvested seeds and harvested seeds were combined for analysis (Appendix S2: Fig. S5). However, high dispersal success does not necessarily directly translate to ultimate recruitment success for the seedling to sapling transition. Seedlings emerging from large-sized seeds are more likely to have higher fitness at the post-seedling stage (Leishman et al. 2000). Nevertheless, plants face a trade-off between seed size and seed numbers (Smith and Fretwell 1974, Venable 1992, Eriksson and Jakobsson 1999, Turnbull et al. 1999, Brancalion and Rodrigues 2014). Plants that produce a large amount of seeds typically produce smaller seeds. Although the survival rate of small-sized seeds may be small, but the absolute number of survived seeds may be higher than medium- and large-sized seeds. Therefore, such a trade-off between seed size and number may alter seed size selection during the seed dispersal stage. Further analysis indicated that the seed size frequency distribution within the species of *P. kerrii* followed a bell-shaped curve where seeds weighing about 5 g had the highest frequency (Appendix S3: Fig. S1a). The absolute number of surviving seeds weighing about 5 g was also highest in our study (Appendix S3: Fig. S1b,c). ANOVA analysis indicated that variances of seed mass among trees of *P. kerrii* ($n = 30$) and within trees were 1,015.616 and 765.329, making up 57% and 43%, respectively, suggesting the variation among trees was very large (Appendix S4: Tables S1, S2). Thus the observed selective pressure would have biological meaning in seed size evolution of *P. kerrii* in nature.

The optimal seed sizes may vary in different dispersal systems or under different conditions. In general, intermediate seed size might not always be optimal for some other plants. Gomez (2004) found that small seeds had higher dispersal fitness than did large seeds for *Quercus ilex*, which was different from our study. Some studies suggested the body mass of the rodents can affect the predation and hoarding behavior of the rodents (Munoz and Bonal 2008, Tamura and Hayashi 2008). It is possible that small seeds may have higher dispersal success when seeds depend upon dispersal by smaller-bodied rodents and vice versa. Under variable and unpredictable conditions, then a maternal plant's fitness might be maximized by producing a variety of seed sizes. Many plant seeds have a very low chance of establishment without being cached by animals (Howe and Smallwood 1982,

Augspurger 1984, Howe et al. 1985, Schupp 1988). However, *P. kerrii* seeds evinced a strong capacity of seedling establishment even if they were not dispersed or damaged by rodents (Cao et al. 2011*b*), suggesting the regeneration strategy of *P. kerrii* may be different from some other plants. It is likely that the medium seed size might not be best for some other plants. Thus, the relationship between seedling establishment and seed size should be more broadly considered across plant species, to further elucidate seed size evolution of plants.

Conclusion

Seed size selection under rodent predation and dispersal is a complex process. We found that seeds experience conflicting selective pressures at the pre- and post-removal stages. Small-sized seeds were more frequently eaten at the early dispersal stage, while large-sized seeds were more likely to be eaten and pilfered (or larger-hoarded) at the late dispersal stage, which resulted in highest dispersal success of medium-sized seeds.

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SUPPORTING INFORMATION