

## ORIGINAL ARTICLE

# Trait-mediated seed predation, dispersal and survival among frugivore-dispersed plants in a fragmented subtropical forest, Southwest China

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## Abstract

By tracking the fate of individual seeds from 6 frugivore-dispersed plants with contrasting seed traits in a fragmented subtropical forest in Southwest China, we explored how rodent seed predation and hoarding were influenced by seed traits such as seed size, seed coat hardness and seed profitability. Post-dispersal seed fates varied significantly among the 6 seed species and 3 patterns were witnessed: large-seeded species with a hard seed coat (i.e. *Choerospodias axillaries* and *Diospyros kaki* var. *silvestris*) had more seeds removed, cached and then surviving at caches, and they also had fewer seeds predated but a higher proportion of seeds surviving at the source; medium-sized species with higher profitability and thinner seed coat (i.e. *Phoebe zhennan* and *Padus braohypoda*) were first harvested and had the lowest probability of seeds surviving either at the source or at caches due to higher predation before or after removal; and small-seeded species with lower profitability (i.e. *Elaeocarpus japonicas* and *Cornus controversa*) had the highest probability of seeds surviving at the source but the lowest probability of seeds surviving at caches due to lower predation at the source and lower hoarding at caches. Our study indicates that patterns of seed predation, dispersal and survival among frugivore-dispersed plants are highly determined by seed traits such as seed size, seed defense and seed profitability due to selective predation and hoarding by seed-eating rodents. Therefore, trait-mediated seed predation, dispersal and survival via seed-eating rodents can largely affect population and community dynamics of frugivore-dispersed plants in fragmented forests.

**Key words:** frugivore-dispersed plants, secondary seed dispersal, seed-eating rodents, seed predation, seed traits

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## INTRODUCTION

Post-dispersal seed fates mediated by seed-eating rodents and other seed predators have fundamental impacts on seedling recruitment, diversity and distribution of frugivore-dispersed plants over time and space (Hulme 1998). Generally, high seed predation levels by

seed-eating rodents may have negative impacts on forest regeneration due to limited seed production in fragmented forests (e.g. Hulme & Hunt 1999; Cramer *et al.* 2007; Velho *et al.* 2012). However, growing evidence indicates that scatter-hoarding rodents can also act as secondary seed dispersers for many frugivore-dispersed plants (e.g. Forget & Milleron 1991; Vander Wall *et al.* 2005; Forget & Cuijpers 2008; Cao *et al.* 2011), as they act as primary seed dispersers for nut-bearing plants. Therefore, it is expected that scatter-hoarding rodents might compensate for seed dispersal and subsequent recruitment of frugivore-dispersed plants at least at local scales, especially when vertebrate frugivores are functionally extinct in a wide range of habitats (e.g. Wright 2003; Cao *et al.* 2011; McConkey *et al.* 2012).

Similar to predator-dispersed plants, such as nut-bearing species, frugivore-dispersed plants also produce seeds varying in seed size, seed defense (e.g. seed coat hardness and chemicals) and seed profitability (food value) (see Moles *et al.* 2003). Thus, rodent seed predation and dispersal may vary considerably among frugivore-dispersed plants, primarily depending on specific traits from their seeds (e.g. Moles *et al.* 2003; Garcia *et al.* 2005). However, how rodent seed predation and dispersal are related to seed traits among frugivore-dispersed plants has been explored little. Compared to other seed traits, seed size is found to cause differential seed predation by rodents (e.g. Moles *et al.* 2003): larger seeds are expected to experience higher predation and lower survival than smaller seeds (e.g. Moles *et al.* 2003; but see Dirzo *et al.* 2007; Mendoza & Dirzo 2007). In contrast, those studies with scatter-hoarding rodents and nut-bearing plants indicate that larger seeds are more likely to be removed and cached (dispersed), rather than eaten *in situ* (e.g. Jansen *et al.* 2004; Xiao *et al.* 2004, 2005, 2006b). Seed coat hardness or thickness may also influence rodent seed predation and dispersal (e.g. Jacobs 1992; Xiao *et al.* 2003, 2005). Zhang and Zhang (2008) show that harder seeds are more likely to be cached but consumed less at the source. Seed profitability (e.g. edible seed kernel proportion) is often the reverse of seed defense, and, thus, higher-profitability seeds are expected to experience higher predation (e.g. Moles *et al.* 2003) or higher dispersal (i.e. more seeds scatter-hoarded) (e.g. Jansen *et al.* 2004). Therefore, selective predation and dispersal by seed-eating rodents may impose strong selection on frugivore-dispersed seeds and vegetation dynamics (e.g. Moles *et al.* 2003; Mendoza & Dirzo 2007; Jorge & Howe 2009; Melo *et al.* 2010; Velho *et al.* 2012).

In this study, we explore how seed predation and scatter-hoarding by rodents influences seed survival among frugivore-dispersed plants with contrasting seed traits in a fragmented subtropical forest in Southwest China. In the study site, frugivorous birds are important seed dispersers for many fleshy-fruited plants producing smaller seeds (Jiang *et al.* 2010). However, due to intense hunting and other human disturbance, most large mammals (e.g. frugivorous primates and deer) are locally extinct, and *Paguma larvata* (C. E. H. Smith, 1827) is the only mammal species known to feed on fruits and to defecate intact seeds. Recently, using camera traps (Ltl Acorn 5210), we found that *P. larvata* can visit many fleshy-fruited plants (over 10 species recorded, including those with larger seeds [e.g. *Choerospondias axillaries* and *Diospyros kaki* var. *silvestris*]). Frugivore-dispersed seeds are also found to be consumed by rodents, and some seeds are cached in surface soil or under leaf litters. Thus, we expected that scatter-hoarding rodents such as *Leopoldamys edwardsi* (Thomas, 1882) (see Xiao *et al.* 2003, 2008; Cheng *et al.* 2005; Chang & Zhang 2011) might act as secondary seed dispersers for some frugivore-dispersed plants. Here, 6 common frugivore-dispersed plants are studied: *C. axillaries* and *D. kaki* var. *silvestris*, which were primarily dispersed by mammals (here, *P. larvata*), and *Phoebe zhenman*, *Padus braohypoda*, *Elaeocarpus japonicas* and *Cornus controversa*, which were primarily dispersed by both mammals and birds. Fruits and seeds of these seed plants varied in size, color, seed defense and food value (Table 1). We addressed the following specific questions:

1. How are selective predation and dispersal by rodents related to seed traits of frugivore-dispersed plants (e.g. seed size, seed coat hardness and seed profitability)?
2. How do differential seed predation and hoarding by seed-eating rodents affect population and community dynamics of frugivore-dispersed plants in forest fragments?

## MATERIALS AND METHODS

### Study site and study species

This study was performed in the Banruosi Experimental Forest (altitude 700–850 m, 31°4'N, 103°43'E) in Dujiangyan City of Sichuan, Southwest China during autumn of 2008 and spring of 2009. The Experimental Forest is highly affected by human disturbance, including farming, logging and hunting. The study site has subtropical forest-type vegetation, but many com-

**Table 1** Population density, fruit/seed traits and dispersal agents of fleshy-fruited species studied

Description	<i>Choerospondias axillaris</i>	<i>Diospyros kaki</i> var. <i>silvestris</i>	<i>Phoebe zhennan</i>	<i>Padus braohypoda</i>	<i>Elaeocarpus japonicas</i>	<i>Cornus controversa</i>
Population density	Low but aggregated	Rare	Low and frequently extracted	Rare	Dominant	Dominant
Fruit color	Orange	Orange	Purple	Black	Purple	Purple
Fresh fruit mass (g)	8.04 ± 1.69 (30)	13.05 ± 2.96 (30)	0.55 ± 0.07 (30)	0.57 ± 0.11 (22)	0.34 ± 0.05 (30)	0.17 ± 0.03 (30)
Fresh seed mass (g)	1.30 ± 0.31 (30)	0.60 ± 0.13 (185)	0.33 ± 0.06 (30)	0.29 ± 0.05 (30)	0.14 ± 0.02 (30)	0.056 ± 0.01 (30)
Number of seeds per fruit	1 (30)	5.1 ± 1.58 (30)	1 (30)	1 (30)	1 (30)	1 (30)
Seed profitability (edible proportion)	Low (<20%)	High (>80%)	High (84.5%)	High (62%)	Low (30.8%)	Low (<20%)
Primary seed disperser	Mammals	Mammals	Birds, mammals	Birds, mammals	Birds, mammals	Birds, mammals
Secondary seed disperser	Rodents	Rodents	Rodents	Rodents	Rodents	Rodents

Mean ± SE (*n*)

mon tree species have become very rare or even extinct in forest fragments due to logging. The weather is often cloudy and foggy, with a mean annual temperature of 15.2 °C, an annual precipitation of 1200–1800 mm and annual hours of sunlight typically in the range 800–1000. The dominant canopy tree species include *Quercus serrata*, *Quercus variabilis*, *Castanopsis fargesii*, *Lithocarpus harlandii*, *E. japonicas* and *Co. controversa*, with only a few individuals of *Pinus massoniana* and *Ph. zhennan* remaining as a result of frequent logging. The understory layer is mainly composed of *Symplocos stellaris*, *Symplocos laurina*, *Ilex purpurea* and *Myrsine africana*.

We selected 6 frugivore-dispersed plants: *C. axillaris*, *D. kaki* var. *silvestris*, *Ph. zhennan*, *Pa. braohypoda*, *E. japonicas* and *Co. controversa*. *E. japonicas* and *Co. controversa* were common in the study site and widely distributed in most of forest fragments, while the other 4 species were relatively rare and had a limited population or distribution. These target plants produce fruits from Aug to Nov. Only *D. kaki* var. *silvestris* have 2–8 seeds per fruit, and other species produce only 1-seed fruits. Fruits and seeds of both *C. axillaris* and *D. kaki* var. *silvestris* were larger (with hard seed coats) than any of those of the other species, but the edible seed kernel proportions of *D. kaki* var. *silvestris*, *Pa. braohypoda* and *Ph. zhennan* were higher (>60%) than in the other species (Table 1). According to our recent camera trapping and focal-tree observations, *P. larvata* was the only known frugivorous mammal, but over 20 frugivorous birds were found in the study sites [e.g. *Pycnonotus sinensis* (J. F. Gmelin, 1789), *Spizixos semitorques* Swinhoe, 1861, *Hypsipetes leucocephalus* (J. F. Gmelin, 1789) and *Garrulax sannio* Swinhoe, 1867] (Jiang et al. 2010). Compared to frugivorous birds, *P. larvata* visited target fruiting plants less frequently (*n* = 20–30 per plant species), although it can consume the fruits of all the target species. During our past and ongoing survey (2000–present), approximately 3–5 *P. larvata* individuals have been hunted each year. This may be the main reason that the *P. larvata* population in the study site is low and would be hard to restore. However, several rodent species were common, including Edward's long-tailed rat (*L. edwardsi*), chestnut rat [*Niviventer fulvescens* (Gray, 1847)], white-bellied rat [*Niviventer confucianus* (Milne-Edwards, 1871)], Himalayan rat [*Rattus nitidus* (Hodgson, 1845)], Norway rat

[*Rattus norvegicus* (Berkenhout, 1769)], Sichuan field mouse (*Apodemus latronum* Thomas, 1911), Chevri-er's field mouse [*Apodemus chevrieri* (Milne-Edwards, 1868)], South China field mouse [*Apodemus draco* (Barrett-Hamilton, 1900)], striped field mouse [*Apodemus agrarius* (Pallas, 1771)] and harvest mouse [*Micromys minutus* (Pallas, 1771)] (Xiao *et al.* 2002, unpubl. data). These rodents feed and/or hoard nuts and seeds from nut-bearing plants (mostly Fagaceae) and some fleshy-fruited plants (Xiao *et al.* 2003, 2005).

### Seed predation and dispersal experiment

After fruits ripened, we collected fruits (seeds) of the 6 tree species from the ground or directly from fruiting plants. Seeds were washed with water for seed predation and dispersal experiments. We randomly selected 360 sound seeds from each species (for a total of 2160 seeds), and all seeds were marked by attaching a small coded plastic tag to each seed through a 10 cm thin wire (see details in Xiao *et al.* 2006a).

We selected 4 separated secondary stands (stand area approximately 1–3 ha) as experimental plots for seed predation and dispersal experiments. For each experimental plot, we established 3 cafeteria stations 20–30 m apart along a transect line and placed 180 tagged seeds at each cafeteria station (i.e. 30 seeds for each seed species on the ground within an area of 1 m<sup>2</sup>). We tracked and recorded the fate of each tagged seed at 1, 2, 3, 5, 7 and 19 weeks after seed exposure. Seed fate at the source (stations) were categorized as survival *in situ*, eaten *in situ* and removed. Those removed from stations were categorized as dispersed (cached in soil or beneath leaf litters, left in the surface), eaten or missing (fate unknown). During each survey, we recorded the distances of eaten and cached seeds after they were removed from seed stations, and used numbered bamboo sticks to mark the cached seeds. At subsequent surveys, we checked all the previous marked tagged seeds. If a marked seed was removed, the area around the cache was extensively searched. At the last visit, we retrieved all the seeds that we could find and recorded seed fate and distances from seed stations.

### Monitoring seed-eating rodents

Surveys for seed-eating rodents were conducted in the same stands used for the seed predation and dispersal experiments in Oct 2008 (slightly earlier than the experiments). We trapped seed-eating rodents using large wired cage traps (30 × 25 × 20 cm, of our own design

approved by the Institute of Zoology, Chinese Academy of Sciences), baited with chestnuts and small pieces of cabbage as food and water. Dry leaves of local species were provided as nest materials. For each stand, we set 40 traps along 2 or 3 trap lines for 3 consecutive nights. Each trap and each trap line were set 10–15 m apart. Traps were placed at 1800–1900 hours in the evening and were checked 12 h later. All captured animals were identified to species, sex and reproductive status (females pregnant, lactating or not; males with testes descended or not). Individuals were then marked with a colored paint to allow identification during the 3-day survey, if they were recaptured. We released each animal at their original point of capture.

### Data analysis

For seed fate data (pooled for each stand), the following variables from source to cache sites were considered: (i) the proportion of non-dispersed and not eaten seeds at each stand (i.e. survival at the source); (ii) the proportion of seeds removed at each stand (the following spring) (i.e. removal from the source); (iii) the proportion of seeds cached in primary caches after removal (i.e. dispersed); and (iv) the proportion of seeds finally surviving for all cached seeds the following spring (i.e. survival at caching sites). Because the above seed fate data were proportion data, generalized linear mixed-effects models were used to test their differences, with a logit link function and seed species as a fixed factor and stand as a random factor.

In this study, we used Kaplan–Meier survival analysis to calculate the mean time (weeks) to seed harvest from seed stations for each seed species and each stand. The mean distance of primary caches or eaten seeds after removal from the source were also calculated for each seed species and each plot. One-way analysis of variance was used to compare the difference in the mean time (log-scale) to seed harvest from seed stations among the 6 seed species, and two-way analysis of variance was used to compare the difference in the mean distance (log-scale) with seed species and seed fate (dispersed *vs* eaten after removal). The  $\chi^2$ -test was used to test the difference in trap success of all rodent species among the 4 stands.

Generalized linear mixed-effects models were carried out using the R program (version 2.8.1), and other statistical analyses were conducted using SPSS for windows (version 10.0).

## RESULTS

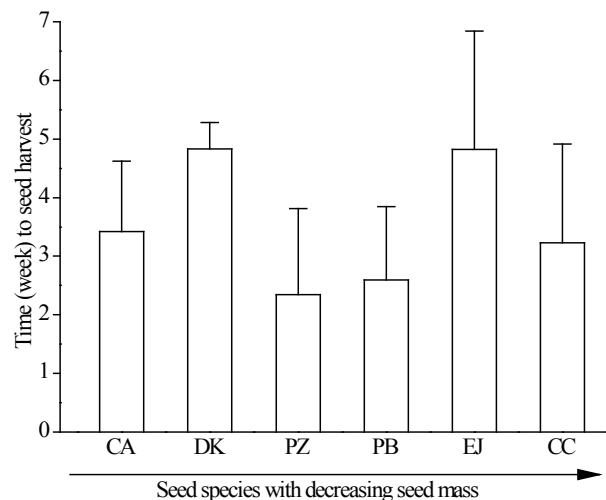
### Seed predation, dispersal and survival

During the experimental period, rodents differentially harvested (either consumed or removed) the seeds at each stand: seeds from *Ph. zhennan* and *Pa. braohypoda* were harvested first and suffered higher predation, compared to the other 4 species (Figs 1 and 2). The mean lifetime of the tagged seeds at seed stations varied significantly among seed species (Wald = 159.691, df = 5,  $P < 0.001$ ): *Ph. zhennan* and *Pa. braohypoda* seeds had the shortest lifetime, but *D. kaki* var. *silvestris* and *E. japonicas* seeds had the longest lifetime (Fig. 1).

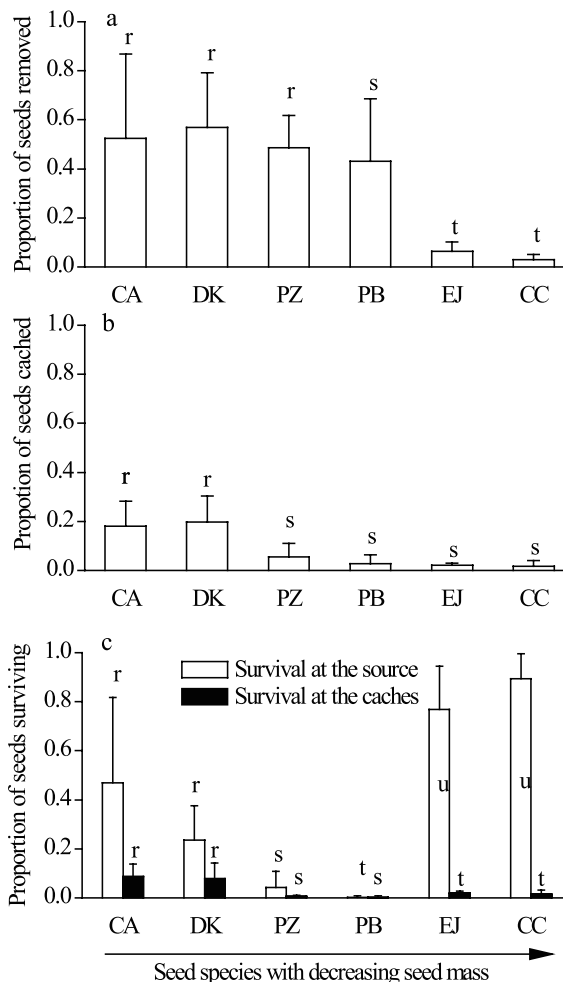
For all 6 seed species, 35.1% of the tagged seeds were removed from seed stations, while 8.3% of the tagged seeds were dispersed (i.e. scatter-hoarded) after removal. We relocated most (88.3%) of the removed seeds. The proportion of seeds removed from seed stations varied significantly among seed species ( $z = 10.989$ ,  $P < 0.001$ ): *D. kaki* var. *silvestris* had the highest removal proportion (57%), followed by *C. axillaris* (53%), *Ph. zhennan* (49%) and *Ph. braohypoda* (43%), with no more than 6% for *E. japonicas* and *Co. controversa* (Fig. 2a). After removal, the proportion of dispersed seeds also varied significantly among seed species ( $z = 5.914$ ,  $P < 0.001$ ): 19.7% of *D. kaki* var. *sil-*

*vestris* seeds were dispersed, followed by *C. axillaris* (18.1%) and *Ph. zhennan* (5.6%), but the rest of the 3 seed species had less than 5% of seeds dispersed (Fig. 2b).

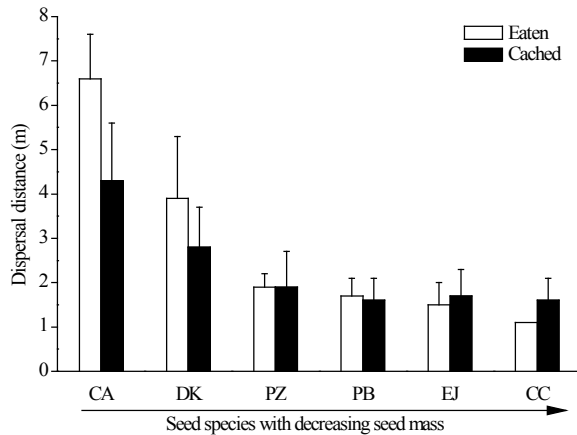
At the end of this experiment (approximately 5 months), 5 of the 6 seed species had part of the seeds



**Figure 1** The time (weeks, mean  $\pm$  SD) to seed harvest at the source (seed stations) after placed for 7 weeks among 6 seed species. CA, *Choerospodias axillaris*; CC, *Cornus controversa*; DK, *Diospyros kaki* var. *silvestris*; EJ, *Elaeocarpus japonicus*; PB, *Padus braohypoda*; PZ, *Phoebe zhennan*.



**Figure 2** Seed fate (proportion, mean  $\pm$  SD) among 6 seed species across different dispersal stages: (a) removed from the source (seed stations); (b) dispersed in caches, including intact seeds buried in the soil or under leaf litter; and (c) final survival of seeds either at the source (i.e. survival at the source) or at caches (survival at caches). CA, *Choerospodias axillaris*; CC, *Cornus controversa*; DK, *Diospyros kaki* var. *silvestris*; EJ, *Elaeocarpus japonicus*; PB, *Padus braohypoda*; PZ, *Phoebe zhennan*. Bars with the same letter are not significantly different ( $P > 0.05$ ).



**Figure 3** Dispersal distances (m, mean  $\pm$  SD) of seeds eaten or cached after removed from seed stations among 6 seed species: CA, *Choerospodias axillaris*; CC, *Cornus controversa*; DK, *Diospyros kaki* var. *silvestris*; EJ, *Elaeocarpus japonicus*; PB, *Padus braohypoda*; PZ, *Phoebe zhenan*.

surviving at the source. The proportion of seeds surviving at the source varied significantly among seed species ( $z = 11.735$ ,  $P < 0.001$ ): 2 small-seeded species (*Co. controversa*, 89.4%; *E. japonicas*, 76.9%) had the highest proportion of seeds surviving at the source, but *Pa. braohypoda* (0%) and *Ph. zhenan* (4%) had the lowest proportion. The proportion of seeds surviving at caching sites also varied significantly among seed species ( $z = 3.902$ ,  $P < 0.001$ ): the 2 large-seeded species with hard seeds (*C. axillaris* and *D. kaki* var. *silvestris*) had the highest proportion of seeds surviving at caching sites, but *Ph. zhenan* and *Pa. braohypoda*, with higher prof-

itability, had the lowest proportion of seeds surviving at caching sites due to strong predation and less hoarding (Fig. 2).

The mean dispersal distance was similar ( $F_{1,25} = 0.065$ ,  $P = 0.479$ ) between eaten seeds and hoarded seeds after they were removed from the source (Fig. 3). However, the mean dispersal distance varied significantly among seed species ( $F_{5,25} = 13.032$ ,  $P < 0.001$ ): *C. axillaris* seeds had the longest mean distance and *D. kaki* var. *silvestris* seeds ranked second, with the dispersal distance of these 2 seed species being 2–3 times longer than that of any other seed species (Fig. 3).

### Seed-eating rodents

Five rodent species were trapped over 120 trap nights across 4 secondary stands: *L. edwardsi*, *N. confucianus*, *N. fulvescens*, *A. latronum* and *A. draco* (Table 2). The total trap success of these rodents was similar among the 4 stands ( $\chi^2 = 0.464$ ,  $df = 3$ ,  $P = 0.927$ ; Table 2).

### DISCUSSION

In this study, our results showed that 2 seed species (*Ph. zhenan* and *Pa. braohypoda*) received extremely higher predation (95%–100%), although a tiny portion (<4%) of their seeds were also scatter-hoarded. Another 2 seed species (*C. axillaries* and *D. kaki* var. *silvestris*) had approximately 20% of seeds scatter-hoarded and most of these hoarded seeds survived at caching sites. In the study site, our previous and ongoing survey (2000–present) has shown that seed-eating rodents are the main seed predators for nut-bearing plants (Xiao *et al.* 2003, 2005, 2006b, 2008). Moreover, our field experiments and behavioral experiments in large enclosures have

**Table 2** Seed-eating rodents captured in each separated stand ( $n = 120$  traps for 3 consecutive nights) used for seed predation and dispersal experiments in Oct 2008 (before the experiments)

Rodent species	Scatter-hoarding†	Stand			
		A	B	C	D
<i>Leopoldamys edwardsi</i>	Yes	2	1	1	2
<i>Niviventer confucianus</i>	No	3	0	1	0
<i>Niviventer fulvescens</i>	Not frequently	0	4	1	0
<i>Apodemus latronum</i>	Not frequently	0	0	1	0
<i>Apodemus draco</i>	Not frequently	1	2	1	5
Trap success (%)		5.00	5.83	4.17	5.83

†Sourced from Xiao *et al.* (2003, 2008, unpubl. data); Cheng *et al.* (2005) and Chang and Zhang (2011).

identified that *L. edwardsi* is the primary scatter-hoarder (seed disperser) for nut-bearing species compared with other rodent species (e.g. *Niviventer* spp. and *Apodemus* spp.) (Xiao *et al.* 2003, 2008; Cheng *et al.* 2005; Chang & Zhang 2011). Therefore, the 5 rodent species trapped in this study are most responsible for seed predation of frugivore-dispersed plants, but scatter-hoarding rodents (primarily *L. edwardsi*) are also important for secondary seed dispersal and subsequent survival of some frugivore-dispersed plants (see below).

Our results also showed that post-dispersal seed fates varied greatly among the 6 seed species, and rodent seed predation and hoarding are highly determined by seed traits of frugivore-dispersed plants. Our study further confirmed that seed size had pronounced impacts on seed removal, seed dispersal (scatter-hoarding and dispersal distance) and seed survival (Figs 2 and 3). This is most consistent with our previous studies with nut-bearing plants in the same study site: larger seeds are more likely to be removed, hoarded and to survive as seedlings than smaller seeds (Xiao *et al.* 2003, 2005, 2006b). However, we found that smaller seeds from *E. japonicas* and *Co. controversa* with lower profitability experienced extremely lower predation levels and had the highest survival probability at the source. This indicates that the smaller seeds (<0.2 g) produced by many frugivore-dispersed plants have a significant advantage for better dispersal by vertebrate frugivores (frugivorous birds in particular) and/or escaping from rodent seed predation, although they do not have the advantage for secondary dispersal by scatter-hoarding rodents (see Vander Wall & Beck 2012). In this study, higher profitability (edible proportion) and lower physical defense (thinner seed coat) explain why medium-sized seeds (i.e. *Ph. zhennan* and *Pa. braohypoda*) experienced higher predation level and much lower survival both at the source and at caching sites. In addition, harder seeds such as *C. axillaries* and *D. kaki* var. *silvestris* had lower predation levels, although these seeds are also larger and even more profitable (i.e. *D. kaki* var. *silvestris*). This is consistent with our previous study that hard nuts from *Li. harlandii* are less predated but hoarded more in the same study site (Xiao *et al.* 2005; Xiao & Zhang 2006).

Due to forest fragmentation and human disturbance (e.g. hunting), many medium/large frugivorous mammals and birds are found to decline dramatically or to be locally extinct (e.g. Corlett 2002; Wright 2003; McConkey *et al.* 2012). Compared with population decline or local extinction of many vertebrate frugivores, however,

many seed-eating rodents suffer little from hunting and are less sensitive to habitat changes in fragmented forests (e.g. Wright 2003; Dirzo *et al.* 2007). According to our study, selective predation and dispersal by seed-eating rodents may have strong impacts on seed survival among frugivore-dispersed plants and thus drive plant population and community dynamics in fragmented forests. In this study, 3 patterns of seed predation, dispersal and survival were recognized for the 6 frugivore-dispersed plants.

### Large-seeded species with hard seeds

Large-seeded species with hard seeds (i.e. *C. axillaries* and *D. kaki* var. *silvestris*) had more seeds removed, cached and then surviving at caches. They also had fewer seeds predated but a relatively higher proportion of seeds surviving at the source. Thus, scatter-hoarding rodents can have positive effects on secondary seed dispersal and subsequent survival for some frugivore-dispersed plants producing large seeds and/or high-defense seeds. Moreover, secondary seed dispersal by scatter-hoarding rodents can compensate for limited seed dispersal of these frugivore-dispersed plants in fragmented forests where medium/large vertebrate frugivores are locally extinct (Wright *et al.* 2007; McConkey *et al.* 2012).

### Medium-sized species with higher profitability and thinner seed coat

Medium-sized species with higher profitability and thinner seed coat (i.e. *Ph. zhennan* and *Pa. braohypoda*) were first harvested and had the lowest probability of seeds surviving either at the source or at caches due to higher predation before or after removal from the source. Obviously, heavy seed predation by seed-eating rodents can have significantly negative effects on seed survival and seedling recruitment of these frugivore-dispersed plants producing high-profitability seeds, especially when populations of these plants are small and seed crops are also limited in fragmented forests. This is consistent with the fact that both *Ph. zhennan* and *Pa. braohypoda* had much lower populations in the study site.

### Small-seeded species with lower profitability

Small-seeded species with lower profitability (i.e. *E. japonicas* and *Co. controversa*) had the highest probability of seeds surviving at the source but the lowest probability of seeds surviving at caches due to lower

predation at the source and lower hoarding. This may be one key reason that these small-seeded species are dominant in the study site compared with the other 4 species.

## CONCLUSION

In conclusion, our study had shown that post-dispersal seed fate varied greatly among the 6 seed species and patterns of seed predation, dispersal and survival among frugivore-dispersed plants are highly determined by seed traits, such as seed size, seed defense and seed profitability, due to selective predation and hoarding by seed-eating rodents. Obviously, our results suggest that for frugivore-dispersed species, seed size may combine other seed traits (e.g. seed defense and seed profitability) to affect seed selection (predation and hoarding) by seed-eating rodents and other seed predators, which, in turn, largely influences seed survival, seedling recruitment and vegetation diversity. Therefore, trait-mediated seed predation, dispersal and survival via seed-eating rodents may drive population and community dynamics of frugivore-dispersed plants in fragmented forests.

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