

Scatterhoarding of Manchurian walnut *Juglans mandshurica* by small mammals: response to seed familiarity and seed size

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Abstract Dispersal patterns can be affected by seed familiarity and seed traits, including size, mass, and nutritional value, but these factors have not been intensively studied in the context of seed dispersal processes. Our aim was to study how small rodents respond to seed size and seed familiarity in their pattern of Manchurian walnut (*Juglans mandshurica*) seeds in two different habitats in temperate forests of northeast China. Our results demonstrated that *Apodemus peninsulae* acts as the most important disperser for Manchurian walnut seeds. Inexperienced small rodents did not reject seeds of the Manchurian walnut and show similar seed removal rates as compared with experienced rodents. Both experienced and naïve rodents actively participated in seed scatterhoarding of Manchurian walnut seeds. Consecutive survey showed that seeds with large size/mass were removed faster than those with small size/mass, indicating a preference for large seeds. However, small seeds scatter-hoarded by small rodents were transported farther than large ones, failing to support the traditional optimization models for various tree species. Small seeds of Manchurian walnut in caches were less likely to be recovered than large ones and showed greater

cache survival rates, indicating that small seeds would be more advantageous for regeneration than large seeds in small rodent-dominated forests.

Keywords Seed dispersal · *Juglans mandshurica* · Caching experience · Seed size · *Apodemus peninsulae*

Introduction

Seed dispersal has long been a great interest to ecologists, particularly in the last three decades (Price and Jenkins 1986; Despain 2001; Zhang and Wang 2001; Medjibe and Hall 2002; Li and Zhang 2003; Gómez 2004; Hollander and Vander Wall 2004; Xiao et al. 2004a, b). Many theoretical and empirical advances have recently been made for seed dispersal processes (Vander Wall 1990; Kitajima and Fenner 2000; Jansen and Forget 2001; Smallwood et al. 2001; Vander Wall 2001; Hulme and Benkman 2002). Small rodents have significant impacts on tree regeneration and are pivotal in the regeneration and demography of large-seeded trees in these processes (Vander Wall 1990; Jansen et al. 2002; Roth and Vander Wall 2005). For this reason, seed selection by rodents has been studied extensively (e.g., Moore and Swihart 2006; Steele et al. 2006; Li and Zhang 2007; Moore et al. 2007; Zhang et al. 2008). It has been demonstrated that learning influences food choosing in a wide range of animals (Estes et al. 2003; Darmaillacq et al. 2004; Villalba et al. 2004; Bernays and Bright 2005). However, the evolutionary and ecological aspects of learning in food selection by rodents are still less understood under natural conditions (Dukas 2004). Takechi et al. (2009) report that mice from habitats with walnut trees tend to eat nuts more efficiently than those who do not experience walnut seeds, and artificial addition of walnut

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seeds increases the proportion of mice able to eat walnuts frequently and efficiently, reflecting improved walnut-feeding skills with experience. Takahashi and Shimada (2008) prove that experienced mice discriminate against tannins significantly; however, inexperienced mice in the group do not show significant selectivity against tannins. Another study shows a strong innate basis in the hoarding decisions of grey squirrels (*Sciurus carolinensis*) foraging on red and white oak acorns (Steele et al. 2006). Steele et al. (2006) also suggest that caching decision by small rodents would be influenced by seed familiarity. On the other hand, dispersal patterns can be affected by seed properties, but these factors have not been well studied in the context of plant dispersal processes, inhibiting effective management and ecological understanding of seed dispersal. The seed-size variation of Manchurian walnut ranges from 4.40 to 15.08 g in mass and 3.20 to 5.40 cm in length, which may be differentially dispersed by scatter-hoarding rodents, as there is a seed-size-mediated interaction with dispersal mode (Tamura and Hayashi 2008). Seeds of Manchurian walnuts, characterized by hard husk and lower tannin content, are much more nutritious than other large-seeded species. Differences in physical and chemical seed traits also play a vital role in determining seed predation, dispersal, and seedling establishment (Steele et al. 2006). Selective consumption of walnut can be applied to seed and seed disperser interactions due to fragmentation of Manchurian walnut forests. However, we have little information about the relationship between seed dispersal patterns and seed size of Manchurian walnut.

In the present study, we sought to determine: (1) If naïve rodents remove and scatter-hoard the same proportion of Manchurian walnut as experienced ones; (2) If seed size plays an important role in dispersal and scatterhoarding of Manchurian walnut by small rodents. The main purpose of the present study is to assess the role of innate basis in seed scatterhoarding by small rodents, and the ecological consequences of seed size on seed dispersal. Based on our field studies, we discuss why the evolution of innate basis and the ecological significance of seed size might have been favored in seed scatterhoarding by small rodents.

Study area and study species

The study was conducted at the end of seed rain of Manchurian walnut in mid-September 2009 in the Dongfanghong Forestry Center (elevation averaged at 750 m, 45° 58'N, 129°08'E) in Yichun City, Heilongjiang Province, Northeast China. The climate of experimental site is dominated by the north temperate zonal monsoon with severe and long winters and short cool summers. The annual average air temperature is 1.4°C with extremes of

maximum at 37°C and minimum at -40°C. Average annual precipitation averaged at 650 mm, 80% of which falls in the short summer growing season from May to September (Yi and Zhang 2008). The study sites were surrounded by various types of forests including conifer plantation and secondary deciduous forest.

Materials and methods

Small rodent identification

In habitats I, II, and III, we used steel live-traps baited with one peanut to monitor rodent species and their relative numbers in autumn (late September) in 2009. Two transects were selected and trap stations were set at 5-m intervals along each transect for four consecutive nights. Then we determined the species and abundance of captured rodents.

Procedure

We selected two different habitats to examine if there is an effect of experience on caching behaviors of small rodents. Habitat I, where the overstory is dominated by *Juglans mandshurica*, *Fraxinus mandshurica*, *Phellodendron amurese*, and *Betula platyphlla* with a few shrubs of *Corylus mandshurica* in the understory. We consider the rodents in this habitat as experienced (e.g., familiar with walnuts). However, *J. mandshurica* tree is completely absent in habitat II, where the overstory is dominated by *Quercus mongolica*, *Pinus koraiensis* with an understory of *Corylus*. Here, rodents were assumed to be inexperienced (unfamiliar with walnuts). Distance between habitat I and II is estimated at 8 km. A large river partitions the two habitats and blocks free immigration of dispersers. Experiments of dispersal of large and small seeds of *J. mandshurica* were conducted in another habitat in which *J. mandshurica* trees are sporadically distributed, termed as habitat III, 5 km away from habitat I and 7 km from habitat II.

When seeds of Manchurian walnut ripe in early September, we collected them on the ground from more than 20 individual trees, and used the water flotation (Yi and Zhang 2008) to distinguish between sound and insect-damaged/empty seeds. Then we labeled them using slightly modified methods as reported by Zhang and Wang (2001) and Li and Zhang (2003). A tiny hole, 0.5 mm in diameter, was drilled through the endocarp of each seed, without damaging the cotyledon and the embryo. A hard flexible plastic tag (2.5×3.5 cm, <0.3 g) was tied through the hole in each nut using a 10-cm thin steel thread. Each tag was consecutively and discriminatively numbered to make each seed easy to relocate and identify. When rodents buried the seeds in the soil or tree leaves, the tags were often left on the surface of the ground, making them

easy to find. Tagging has negligible effect on seed removal and caching by rodents (Zhang and Wang 2001; Xiao et al. 2006).

In each habitat I and II, 20 plots were established as experimental seed stations, spaced 20-m apart along a transect line. We respectively placed 30 tagged seeds with uniform size at each seed station to evaluate the effect of experience of small rodents on dispersal patterns (total 1,200 seeds). For seed-size-mediated experiments in habitat III, groups of large and small walnut seeds were used after each seed was weighed and measured. In each of the 20 seed stations, ten large and ten small seeds were placed (total 400 seeds). To see the difference in large and small seeds, we randomly selected each 25 of them for seed trait measurement. We then searched the area around each seed station (radius, <20 m), with an equal effort of two people for 10 min per visit. The seed fates can be sorted into six categories: (1) intact in situ, (2) eaten in situ; (3) eaten after removal, (4) intact after removal (on surface; IAR); (5) scatter-hoarded after removal (in soil; CAR); (6) Missed (may be in burrow or not seen). When we found a cache, we measured the distance of the tagged seeds from the seed station. In the next visit, we also checked all the caches relocated in previous visits until the caches were removed or eaten by rodents.

Data analyses

Differences in seed traits (size, mass, and seed profitability) were tested using independent sample *t* test (Yi and Zhang 2008). Cox regression was used to compare the time to removal from seed stations between the two habitats and between large and small seeds (Xiao et al. 2004a). One-way ANOVA was used to test the difference in seed fates between large and small seeds. Independent Sample *T* Test was used to test the difference in seed fates between the two habitats (Yi and Zhang 2008). General Linear Model was used to test the difference in dispersal distances between large and small seeds. The median persistence times of seeds at seed stations in enclosures were analyzed with life table (Zhang and Zhang 2008). Difference in small rodent abundance among the three habitats was detected using nonparametric *k* independent samples tests (Kruskal–Wallis; Zhang 2007).

Results

Small rodent abundance and disperser identification

In late September, three rodent species (totally 17) were trapped over 216 trap nights in habitat I: *Apodemus peninsulae* (12), *Clethrionomys rufocanus* (three), and *Eutamias sibiricus* (two). Twelve were trapped over 165 trap nights in habitat II: *A. peninsulae* (nine), *C. rufocanus* (two), and *E. sibiricus* (one) and 14 were trapped over 204 trap nights in habitat III: *A.*

peninsulae (ten), *C. rufocanus* (two), and *E. sibiricus* (two). No *Sciurus vulgaris* was captured during our survey. There is no difference in the rodent abundance in the three habitats ($\chi^2=0.644$, $df=2$, $P=0.725$). Our recent studies (unpublished data) carried in semi-natural enclosure identified *A. peninsulae* as the only species participating in scatterhoarding seeds of Manchurian walnut. However, *C. rufocanus* only acts as larder–hoarder and consumer, and *E. sibiricus* neither eats nor stores walnuts. Tree squirrel *S. vulgaris* is considered to be the main dispersers of walnuts, however, Korean pine forest fragmentation has affected habitat selection of *S. vulgaris* and led to a severe decline in the abundance of this dispersal agent in our study areas. The role of *S. vulgaris* in dispersing walnuts can be neglected because we witnessed no *S. vulgaris* in our survey.

Seed traits

The fresh weight of large seeds ranged from 9.40 to 15.08 g (11.79 ± 1.36 g, $n=25$, the same as below) and from 3.20 to 5.40 cm in length (4.81 ± 0.22 cm). The small seed weighted from 3.74 to 8.46 g in mass (6.82 ± 0.91 g) and from 3.20 to 4.50 cm in length (3.94 ± 0.33 cm). The maximum width of large and small seeds averaged at 3.41 ± 0.18 cm and 2.66 ± 0.17 cm. There are obvious differences in seed weight, length, maximum width between large and small seeds of *J. mandshurica* ($t=11.916$, $df=48$, $P<0.0001$; $t=8.589$, $df=48$, $P<0.0001$; $t=11.101$, $df=48$, $P<0.0001$). The proportion of edible kernel to the total seed (i.e., seed profitability) averaged at $16.75\pm 1.53\%$ and $14.34\pm 2.10\%$ for large and small seeds respectively, and showed significant difference ($t=2.648$, $df=23$, $P=0.014$). These provide a solid basis for evaluating the effects of seed size/mass on dispersal patterns.

Seed removal and seed fate response to seed familiarity and seed size

Our regular surveys demonstrated that Manchurian walnut seeds were gradually harvested after removal both in habitats I and II (Fig. 1). The median persistence times were 1.92 and 3.58 days for released seeds in habitats I and II, respectively. However, no difference was detected between seed removal rates between the two habitats in which experienced and naïve rodents are distributed (Wald=3.208, $df=1$, $P=0.073$). Although more seeds remained intact in seed stations in habitat II than in habitat I ($t=-7.564$, $df=38$, $P<0.0001$), naïve *A. peninsulae* actively participated in scatter-hoarding seeds of Manchurian walnut compared with experienced ones ($t=-9.675$, $df=38$, $P<0.0001$; Fig. 2). The naïve rodents ate a number of seeds either in situ or after removal in habitat II, however, no seed was found eaten in habitat I.

Consecutive survey indicated that seeds with large size/mass were removed faster than those with small size/mass (Fig. 3).

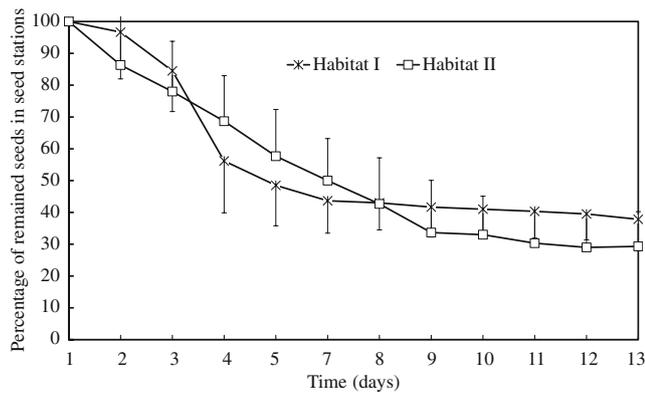


Fig. 1 Seed removal rates of *J. mandshurica* released in habitats I and II. Data were expressed as mean±SE, sample size was 20 both in habitats I and II

Cox regression analyses revealed a significant difference in survival rates between seeds with different properties (Wald=18.878, *df*=1, *P*<0.0001; Fig. 3). One-way ANOVA analyses showed a great proportion of seeds with large size scatter-hoarded by small rodents ($F_{1, 38}=17.213$, *df*=1, *P*<0.0001; Fig. 4), indicating a highly preference for seeds with great mass and large size as well as high seed profitability.

Dispersal distances response to seed familiarity and seed size

Almost 100% of the removed seeds (except for missed seeds) were distributed within 0–10 m per movement around seed stations in habitat I where experienced rodents display (Fig. 5), with an average dispersal distance of 3.64 ± 1.59 m and maximum of 11 m. In habitat II, the naïve rodents moved more than 10% seeds with an average of 4.74 ± 3.41 m and maximum 18 m (Fig. 5). We found an effect of seed size on dispersal distances, the mean transported distances to the cache sites were 4.67 ± 2.37 m for large seeds and 7.48 ± 4.95 m for small seeds and showed

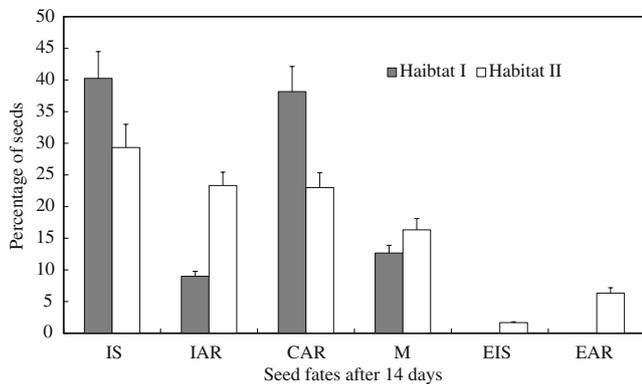


Fig. 2 Seed fates of *J. mandshurica* after primary dispersal by small rodents in habitats I and II. Data were expressed as mean±SE, sample size was 20 both in habitats I and II

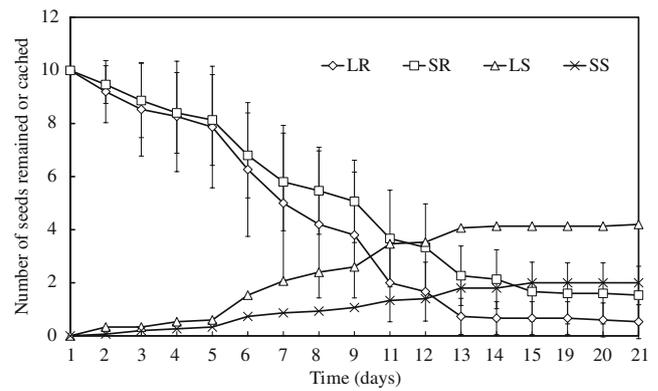


Fig. 3 Survival curves of large and small seeds of *J. mandshurica* in seed stations LR indicates remained large seeds in seed stations, SR refers to remained small seeds in seed stations, LS represents the accumulative scatter-hoarded large seeds, SS stands for the accumulative scatter-hoarded small seeds. Data were expressed as mean±SE, sample size was 20 for both large and small seeds

significant difference ($F=5.028$, *df*=1, *P*=0.027; Fig. 6). However, we witnessed no difference in dispersal distances of seeds remained intact after removal (IAR; $F=3.210$, *df*=1, *P*=0.078), i.e., 4.64 ± 3.20 m and 3.20 ± 1.68 m for large and small seeds, respectively (Fig. 6). General linear model also indicated a great difference between dispersal distances of IAR and CAR in small seeds ($F=10.510$, *df*=1, *P*=0.002), but not in large ones ($F=0.567$, *df*=1, *P*=0.453; Fig. 6).

Cache dynamics and survival response to seed familiarity and seed size

We located 38.17% of seeds for primary caches, 2.83% for secondary caches and 0.16% for third dispersal in habitat I; the corresponding data were 23%, 5.67%, and 0.33% in habitat II, respectively. In caches, 35.83% and 14.67% of seeds survived in habitats I and II till our last survey, respectively. Our results strongly indicated that caches made by small rodents were less likely to be recovered in habitat I than in habitat II. In terms of the

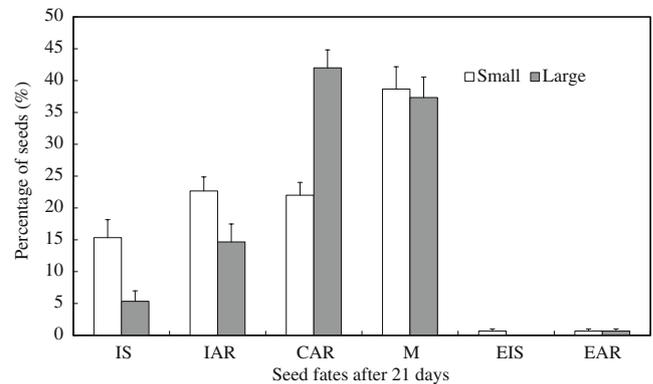


Fig. 4 Seed fates of large and small seeds of *J. mandshurica* after primary dispersal by small rodents. Data were expressed as mean±SE, sample size was 20 for both large and small seeds

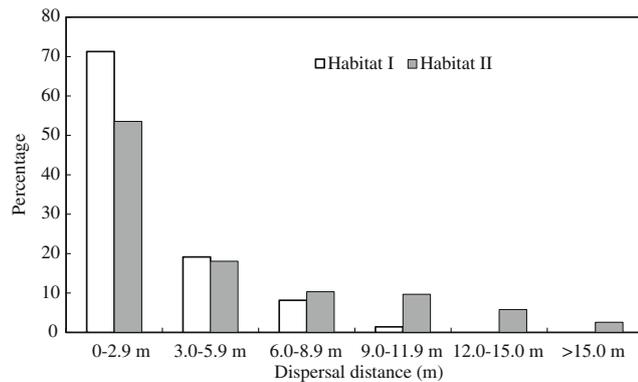


Fig. 5 Frequency distributions of seed dispersal distances of *J. mandshurica* in habitats I ($n=282$) and II ($n=155$)

ecological effect of seed size on dispersal, we found small seeds were less likely to be retrieved than large ones, as indicating from the fact that total 35.33% and 23.33% seeds were re-dispersed in second dispersal for large and small seeds, respectively, and the corresponding data were 9.33% and 4.67% in third dispersal process. Total 17.33% and 15.33% caches survived for large and small seeds till our last survey, respectively.

Discussion

Seed scatterhoarding response to seed familiarity

No significant difference was found in seed removal rates between the experienced and naïves rodents in the two habitats. Both the experienced and naïve *A. peninsulae* actively participated in seed scatterhoarding of Manchurian walnut, indicating the innate basis of small rodents for seed caching. Therefore, individual experience on seeds cannot influence seed choices. Inexperienced rodents do not reject seeds of Manchurian walnut and show similar seed removal rate and caching activity to experienced ones, reflecting an innate basis for seed selection without any training.

However, the proportion of scatter-hoarded seeds and cache survival rates in habitat I were higher than those in habitat II. The ecological consequence is that *A. peninsulae* are unable to efficiently manage all the caches and then leave them more opportunities for survival and seedling establishment (Stapanian and Smith 1978; Vander Wall 1990; Jansen et al. 2004). We found that a small proportion of seeds were eaten in situ or eaten after removal, perhaps because the thicker endocarp of 0.32–0.65 mm measured in Manchurian walnut seeds increases seed handling time for seed-eating animals and thus increases the seed-eaters risk of predation (Jacobs 1992; Hadj-Chikh et al. 1996). Avoiding eating seeds in situ might serve a tactic to escape risk of predation (Vander Wall 1995; Jansen and Forget 2001; Xiao et al. 2003; Vander Wall 2003; Xiao et al.

2006). Few seeds eaten in situ in habitat II generally reflect the innate acclimation of small rodents to seeds with thicker endocarp. All relocated caches contained only one tagged seed of Manchurian walnuts, indicating the same caching strategy of the experienced and naïve rodents. High proportion of one-seed caches indicated lower risk of pilferage, lower sibling competition and more potential sites for seedling establishment.

Seed dispersal by scatter-hoarding rodents response to seed size

It is widely accepted that large seeds are more likely to be scatter-hoarded than small ones (Forget et al. 1998; Vander Wall 2003; Jansen et al. 2004). Moreover, recent studies on seed dispersal by herbivorous rodents have obtained that seeds with large sizes (Forget et al. 1998; Vander Wall 2003; Xiao et al. 2006), higher fat contents (Jansen and Forget 2001; Xiao et al. 2003), and hard hull (Zhang et al. 2005) are more likely to be removed and then scatter-hoarded, rather than eaten in situ. In the present feeding experiments in which small rodents were provided with two different sizes of seeds, large seeds tended to be scatter-hoarded in preference to smaller ones, supporting previous studies (Jansen et al. 2002, 2004). This tendency may be because of the higher profitability or rewards of large seeds, making large seeds worthwhile to be hoarded (Stapanian and Smith 1984; Hurley and Robertson 1987; Vander Wall 1995).

Comparisons of the dispersal distances between seeds with different size and/or preference for target animals have been widely investigated (Stapanian and Smith 1984; Hurley and Robertson 1987; Vander Wall 1995). Although long-distance locomotion incurs higher costs, caching seeds at farther distances and consequent re-caching may be advantageous to animals because of a decreased risk of

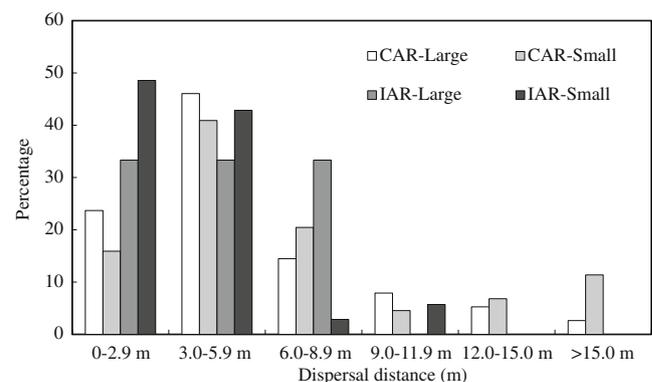


Fig. 6 Frequency distributions of seed dispersal distances of large and small seeds of *J. mandshurica*. CAR-Large indicates scatter-hoarded large seeds ($n=76$), CAR-Small refers to scatter-hoarded small seeds ($n=44$), IAR-Large represents large seeds remained intact after removal ($n=24$), IAR-Small stands for small seeds remained intact after removal ($n=35$)

pilfering and an increased cache recovery rates (Tamura et al. 1999; Moore et al. 2007). Despite theoretical models, seed hoarding predict that larger seeds should be scatterhoarded at greater distances than smaller ones (Stapanian and Smith 1978; Clarkson et al. 1986; Brewer and Webb 2001; Moore et al. 2007), we failed to see this pattern in Manchurian walnut seeds that small seeds were scatterhoarded significantly further than large ones. These results are beyond our expectation and are not consistent with previous studies (Moore et al. 2007). This can be explained by the fact that the walnut seeds in this study were heavy (11.79 g) and large (4.81×3.41 cm) compared to the main disperser *A. peninsulae* (25.09±3.04 g, $n=21$). Seed weight of Manchurian walnut may have been beyond the point at which seed manipulation by *A. peninsulae* becomes increasingly difficult and expensive, decreasing the net benefit of scatterhoarding (Jansen 2003). The differentiation in dispersal distance of large and small seeds of Manchurian walnut may be heavily dependent on body sizes of the main disperser, *A. peninsulae*. Despite that large seeds were highly scatterhoarded more than small ones, more small seeds in caches survived and remained less dynamic. Bigger is not always better (Gómez 2004), and smaller seeds may be advantageous in regeneration if the main seed dispersers are small-sized mice (Tamura and Hayashi 2008). Under the prediction of constant ability of small rodents to recover their caches, we can expect that small seeds of Manchurian walnut would be more advantageous for regeneration than large seeds in the study regions with *A. peninsulae* as dominant disperser.

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