

Seed trait and rodent species determine seed dispersal and predation: evidences from semi-natural enclosures

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Seed traits affect seed dispersal by animals. However, the combined role of seeds and dispersers in determining seed dispersal is not well explored. We attempted to test how seed traits and predators determine seed dispersal and predation interaction in a rodent-mediated seed dispersal system. Semi-natural enclosure experiments were conducted to investigate seed dispersal and predation of five sympatric tree species with different seed traits, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Corylus mandshurica* and *C. heterophylla* by three rodent species, *Apodemus peninsulae*, *Tamias sibiricus* and *Clethrionomys rufocanus* showing different body sizes, hoarding behaviors and activity rhythms. Our results demonstrated that seed species with thick coat were removed more slowly than thin-coated seeds in regardless of rodent species, reflecting a consistent negative effect of seed coat on seed dispersal. Seeds with thick coat were less likely to be eaten both *in situ* and after removal by small rodents. Seeds with high caloric value were more likely to be larder-hoarded, whereas seed traits showed no influence on scatter-hoarding. Rodent species with large body size tended to eat more seeds *in situ*, while small-sized rodents preferred to eat seeds after removal. Large-sized rodent species scatter-hoarded more seeds, however, small-sized rodents larder-hoarded more seeds. Seeds with thick coat showed high mutualism but low predation with rodents, while rodents with large size showed low mutualism but high predation with seeds. Our results indicate that both seeds and predators play important roles in determining seed dispersal and predation in the seed-rodent dispersal system.

Keywords: Body Size, Caloric Value, Seed Coat, Seed Dispersal

Introduction

Many plant species producing large-sized seeds rely substantially on animals for their seed dispersal (Herrera 2002, Jansen et al. 2002, Roth & Vander Wall 2005, Steele et al. 2006, Muñoz & Bonal 2007). In the dispersal systems, animals depend on plant seeds as nutrition supplies for their survival, especially in food shortage periods, and future reproductive success (Vander Wall 1990, O'Farrill et al. 2013). Seed predators may also act as effective seed dispersers, provided that seeds are cached and not completely retrieved (Yi & Yang 2011, Lai et al. 2014, Zhang et al. 2014). Two kinds of seed hoar-

ders can be distinguished according to their caching strategies: larder hoarders usually store food items in central caches; while scatter hoarders store food in spaced caches and invest little to defense stores and reduce pilferage (Vander Wall 1990, Jenkins et al. 1995).

Seed dispersal can be affected by various properties of seeds (e.g., Moore & Swihart 2006, Steele et al. 2006, Li & Zhang 2007, Zhang & Zhang 2008). Seed traits have been recognized as important factors affecting rodents' final decision to manipulate food sources (Kelrick & MacMzhon 1985, Zhang & Zhang 2008, Lai et al. 2014). Seed size

(Moles et al. 2003, Xiao et al. 2005a, Xiao et al. 2013, Barcelos et al. 2013, Capece et al. 2013), handling time (Kaufman & Collier 1981), moisture content (Hulbert & Macmillen 1988), energy and soluble carbohydrates (Kelrick & MacMzhon 1985, Kerley & Erasmus 1991, Xiao et al. 2005b), nutrients (Alexander et al. 2001, Jansen & Forget 2001, Xiao et al. 2006), secondary chemical compounds (e.g., tannins and other polyphenols - Steele et al. 1993), seed coat thickness (Zhang & Zhang 2008, Takechi et al. 2009) as well as seed germination schedule (Xiao et al. 2013) have been identified to show influences on seed removal and dispersal. Apart from the influence of seed traits, environmental factors such as habitat qualities and seasonal variations show great impacts on seed removal and dispersal (Hulme 1997, Kollmann et al. 1998, Wang et al. 2000, Meng et al. 2012).

Sympatric rodent species often differ greatly for instance in body size, tooth morphology, and nutrition requirement, and they may differ in affecting seed fates in the field (e.g., Kerley & Erasmus 1991, Muñoz & Bonal 2008a). Large-sized rodent species may have strong abilities of opening hard seeds, defending food caches or predation, which may affect their seed hoarding strategies. It suggests that larder-hoarding is often adopted by dominant or stronger animals because they can defend their larders (Dally et al. 2006), while scatter-hoarding is generally considered as a strategy of subordinate animals to minimize the risk of catastrophic loss of hoarded food (MacDonald 1997, Preston & Jacobs 2001). Therefore, body size of small rodents may be another important factor in affecting hoarding strategies (e.g., scatter- vs. larder-hoarding). Previous field studies usually evaluated the interaction between seeds and rodents at community levels, as it is impossible to evaluate the role of a single rodent species in seed dispersal of various tree species. Therefore, it is hard to discriminate specific behavioral response of one given rodent species to certain seed traits when selecting seeds (Muñoz & Bonal 2008b, Zhang & Zhang 2008). Although seed trait plays an important role in determining the formation of mutualism and predation interactions among multiple tree and animal species (Zhang & Zhang 2008, Lai et al. 2014, Wang et al. 2014), the effects of both seed and rodent traits on seed dispersal and predation have been not well evaluated (Chang & Zhang 2014).

The purpose of this study is to investigate how three sympatric rodent species with different body sizes affect seed dispersal and seed fates of five sympatric tree species in semi-natural enclosures in northeastern China. We predicted that: (1) thick-coated seeds will be removed more slowly than seeds with

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thin coat because thick coat usually increase the time for rodents to eat seeds (Zhang & Zhang 2008); (2) thick-coated seeds will be less likely eaten *in situ* but more likely eaten after removal according to the handling-time hypothesis; (3) more seeds with high caloric value will be hoarded by rodents according to the optimal forage theory (Pyke 1984); (4) large-sized rodent species will eat more seeds *in situ*, while rodents with small size tend to eat seeds after removal; (5) large-sized rodents will larder-hoard more seeds than small-sized ones, while rodents with small size will scatter-hoard more seeds than large-sized rodents due to their lower ability to defend larders (MacDonald 1976, Preston & Jacobs 2001).

Materials and methods

Study site

This study was conducted in the Dongfanghong Forestry Center (average elevation 750 m, located at 46° 50' to 46° 59' N, 128° 57' to 129° 17' E) in the Dailing district, Yichun city, Heilongjiang Province, north-eastern China. The climate of the experimental site is dominated by the north temperate zonal monsoon with severe and long winters and short summers. The annual average temperature is 1.4 °C with maximum at 37 °C and minimum at -40 °C. Average annual precipitation averages at 660 mm, with 80% of annual precipitation falls between May and September (Yi & Zhang 2008).

Experimental enclosures

Sixteen separate semi-natural enclosures (10 × 10 × 2.5 m) were constructed in an open area at the edge of the forests. The enclosures were built using bricks about 2.5 m above and 0.5 m below the ground. The walls of the enclosures were smoothed to prevent escape of small rodents. Grasses commonly found in the forests were distributed with an average coverage of 60%, while trees and shrubs were removed to prevent rodents from escaping by climbing. To prevent avian predators from entering the en-

losures, the enclosures were covered with plastic nets on the top. An artificial nest constructed of bricks (H × W × L = 20 × 15 × 30 cm) and a plastic water bowl were placed at one corner of the enclosure to allow animals to rest and drink freely. A seed station of 0.5 m² was established at the center of each enclosure.

Tested rodent species

The dominant rodent species in the study site are *Apodemus peninsulae* (Rodentia, Muridae), *Clethionomys rufocanus* (Rodentia, Cricetidae) and *Tamias sibiricus* (Rodentia, Sciuridae). They were chosen for the present experiments because their significant role in the dispersal of large seeds of local tree species (Yi & Zhang 2008). *A. peninsulae* and *C. rufocanus* are small nocturnal species, while *T. sibiricus* is a larger diurnal rodent. *T. sibiricus* mainly scatter-boards but occasionally larder-boards seeds of local tree species, while *A. peninsulae* behaves differently, mainly larder-boarding but sometimes scatter-boarding seeds. Another nocturnal species, *C. rufocanus*, is pure seed predator and only larder-boards seeds of local tree species.

During seed fall in early September 2010, steel frame live traps with a size of 9 × 10 × 25 cm (H × W × L), baited with peanuts and some carrots, were placed in the forests with a 5 m interval along four transects at 9:00 a.m. for animal trapping. We checked the traps every three hours to ensure safety of the captured rodents. All traps were removed at 6:00 p.m. and re-placed next day. Trapping stopped in bad-weather days, such as heavy rain. The target animals captured in each visit were transported by car to the laboratory housing room within no more than 30 minutes. In the laboratory, the animals were individually kept in steel frame cages (H × W × L: 40 × 50 × 90 cm) at outdoors conditions (15-25 °C, 14h of daylight). They were provided with carrots, peanuts, tree seeds and water *ad libitum*. No animal died during trapping and laboratory rearing. The Dailing Forestry Bureau of the Heilongjiang

Province issued permits for the experimental animal trapping. Our behavioral trials and housing procedures were approved by the College of Agriculture, Henan University of Science and Technology. Four days after the experiments, all animals were released where they were captured.

Experimental seeds

The seeds of the five sympatric plant species *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Corylus mandshurica* and *C. heterophylla* were tested (Tab. 1). In the study region, *C. mandshurica* and *C. heterophylla* are dominant shrub species, while *P. koraiensis*, *Q. mongolica* and *J. mandshurica* are dominant tree species. Seeds of these five tree species were reported to be dispersed and predated by *T. sibiricus*, *A. peninsulae*, and *C. rufocanus* (Shen et al. 2012). Seeds of *J. mandshurica* are rich in fat and have the largest size and the thickest coat. *C. heterophylla* produces seeds of medium size and thick coat, while *Q. mongolica* produces medium-sized acorns with thinnest seed coat, low nutrition level and high level of tannins. *C. mandshurica* and *P. koraiensis* have the smallest seeds with thin coat and high nutrition level. During seed fall, seeds of the five species were collected from the ground under 10-15 trees. Thirty seeds of each tree species were randomly selected for the measurement of physical traits (seed mass, seed length, seed width and coat thickness by using electric vernier caliper and precision scale). Ninety seeds of each tree species were dried at 60 °C for 48 hours. The whole kernel of each seed was carefully collected and weighed. Then, thirty kernels of each species were mixed up into a sample for nutrition analyses, therefore a total of three samples were collected. Concentrations of crude protein, crude fat, crude starch and tannin of the seeds were measured by the Cereal Quality Supervision and Testing Centre, Ministry of Agriculture, China (No. 12 Southern Zhong-guancun Road, Haidian District, Beijing). The caloric values of seeds were calculated

Tab. 1 - Morphological and nutritional traits of the five seed species (mean ± SD). These seeds were the same as those in the removal experiments. (*): Data are drawn from Yi & Zhang (2008), Yi et al. (2011), and Yang et al. (2011).

Seed traits	Seed species				
	<i>Juglans mandshurica</i>	<i>Corylus mandshurica</i>	<i>Corylus heterophylla</i>	<i>Quercus mongolica</i>	<i>Pinus koraiensis</i>
Seed size (length × width - cm)	4.19 × 2.89	1.43 × 1.20*	1.58 × 1.44*	2.52 × 1.84	1.60 × 1.11*
Seed mass (g)	13.61 ± 1.28	0.73 ± 0.08*	1.18 ± 0.28*	2.86 ± 0.21	0.73 ± 0.05*
Seed coat thickness (cm)	0.32 ± 0.65	0.11 ± 0.01*	0.24 ± 0.03*	0.05 ± 0.01	0.11 ± 0.01*
Proportion of kernel mass (%)	21.10 ± 0.86	38.57 ± 3.55	18.66 ± 4.29	85.75 ± 1.66	37.03 ± 1.82*
Tannin concentration (%)	0.07 ± 0.01	0.25 ± 0.02*	0.07 ± 0.02*	4.33 ± 0.34	0.02 ± 0.01*
Protein (%)	27.02 ± 0.71	20.30 ± 0.16	28.27 ± 0.11	7.40 ± 0.21	16.18 ± 0.25
Fat (%)	61.11 ± 0.25	47.09 ± 0.14	0.24 ± 0.03	1.76 ± 0.14	37.92 ± 0.46
Starch (%)	0.07 ± 0.07	1.13 ± 0.25	0.00 ± 0	38.27 ± 1.97	0.42 ± 0.06
Caloric value per seed (KJ)	81.61 ± 0.21	6.21 ± 0.02*	4.30 ± 0.03*	20.96 ± 0.97	7.44 ± 0.05*
Caloric value of seed species (KJ/g)	41.63 ± 0.11	17.74 ± 0.05	13.45 ± 0.11	9.52 ± 0.44	29.77 ± 0.19

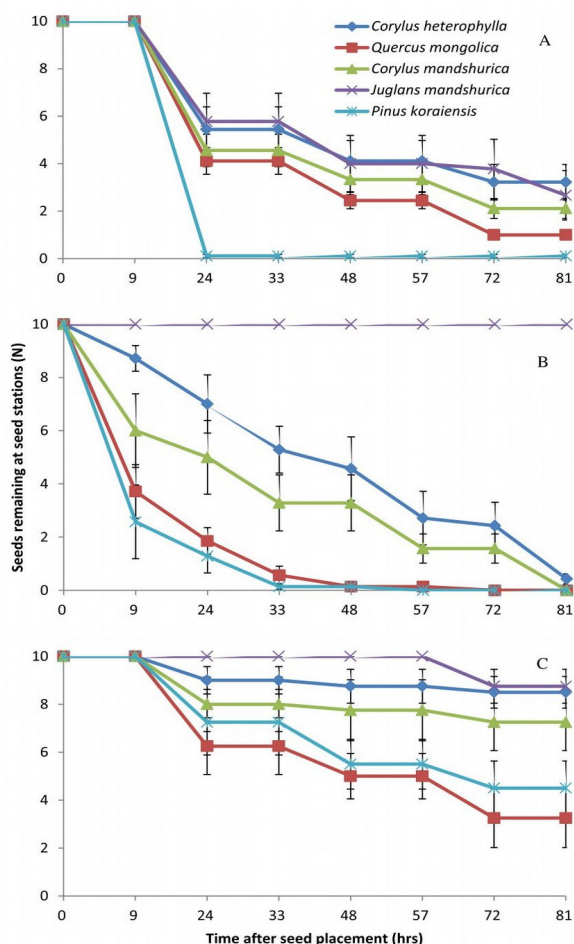


Fig. 1 - Seed removal of five sympatric seed species from seed stations by individual of each rodent species in semi-natural enclosures. (A): *Apodemus peninsulae* (n = 9); (B): *Tamias sibiricus* (n = 7); (C): *Clethrionomys rufocanus* (n = 7). Data are expressed as mean \pm SE.

by the average gross energy equivalents of protein, fat, and carbohydrates. Yang & Xiao (2002) have calculated the corresponding values for the three organic matters, *i.e.*, 17.2 kJ/g, 38.9 KJ/g, and 17.2 kJ/g, respectively. Caloric value per seed was calculated using mean kernel mass \times caloric value of seeds (Zhang & Zhang 2008). The caloric values per seed and per gram kernel were used to reflect the nutritional values of tree species. Seeds were then labeled with plastic tags according to Yi et al. (2011) with minor modifications. A hole (0.3 mm in diameter) was drilled through the seed coat of each seed, without damaging the cotyledon and the embryo. A flexible plastic tag (2.5 \times 3.5 cm, < 0.3 g) was tied through the hole in each seed using a thin 10 cm-long steel thread.

Assessment of seed selection and dispersal by rodents

Trapped animals were starved for 12 hours

before being moved in the enclosures. At 7:00 a.m. one animal was singly introduced in each enclosure to test seed removal, seed predation and hoarding. Nine adult individuals of *A. peninsulae* (5 females, 4 males, body mass: 26.83 \pm 5.64 g, mean \pm SD), 7 *C. rufocanus* (3 females, 4 males, body mass 33.38 \pm 3.57 g) and 7 *T. sibiricus* (3 females, 4 males, body mass: 104.80 \pm 9.25 g) were randomly selected for the seed removal experiments. Ten intact tagged seeds of each tree species were supplied to each individual only once. The tagged seeds in the enclosures were checked in the morning (7:00 a.m.) and afternoon (16:00 p.m.) daily in the following 3 days (81 hours). The seed removal rate by small rodents was reflected by the proportions of intact seed remaining at the seed stations. Scatter-hoarded seeds were located easily because the attached tags are usually left on the ground after being buried by rodents.

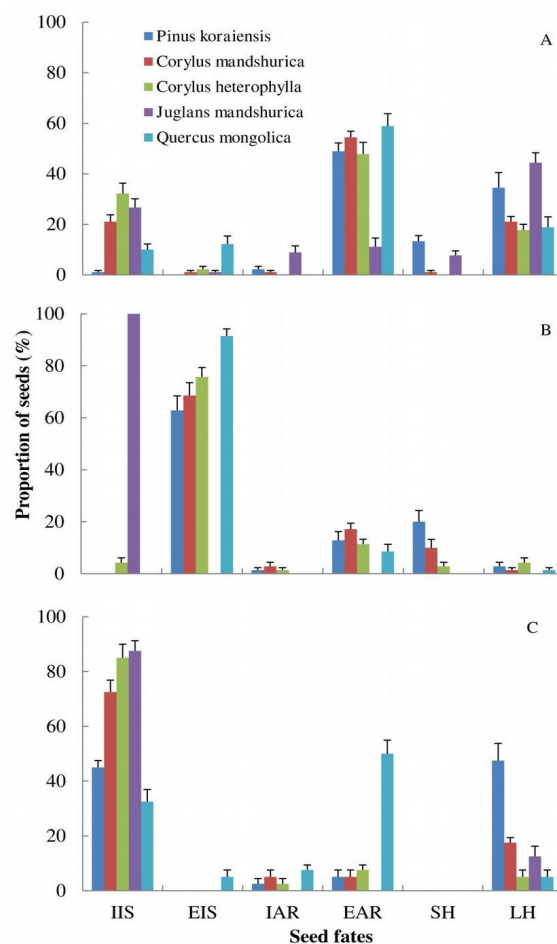


Fig. 2 - Seed fates of five sympatric seed species manipulated by individual of each rodent species in semi-natural enclosures. (A): *Apodemus peninsulae* (n = 9); (B): *Tamias sibiricus* (n = 7); (C): *Clethrionomys rufocanus* (n = 7). (IIS): intact *in situ*; (EIS): eaten *in situ*; (EAR): eaten after removal; (IAR): intact after removal; (SH): scatter-hoarded; (LH): larder-hoarded. Data are expressed as mean \pm SE.

Data analysis

Statistical Package for the Social Sciences (SPSS 16.0) was used for data analyses. Cox regression was used to identify difference in seed removal rates of the five seed species at seed stations. Two-way ANOVA was used to test the effects of plant and rodent species on the number of seeds remaining at seed stations (IIS), eaten *in situ* (EIS), intact after removal (IAR), eaten after removal (EAR), scatter-hoarded (SH) and larder-hoarded (LH), respectively.

Results

Seed removal rate according to plant species

Seed removal rate by *A. peninsulae* was marginally different among the five tested plant species (Wald = 9.34, df = 4, P = 0.053), following the order: *P. koraiensis* > *Q. mongolica* > *C. mandshurica* > *C. hetero-*

Tab. 2 - The effects of seed and rodent species on seed fates of the five sympatric tree species. Data are seed numbers and expressed as mean \pm SD. Different letters in the same column indicate significant difference at $P < 0.05$ among seed or rodent species. Seed fates in the table were defined as: intact *in situ* (IIS), eaten *in situ* (EIS); eaten after removal (EAR), intact after removal (on surface - IAR), scatter-hoarded (SH) and larder-hoarded (LH).

Type	Species	IIS	EIS	IAR	EAR	SH	LH
Seed species	<i>Pinus koraiensis</i>	0.95 \pm 1.85 ^a	2.20 \pm 3.24 ^a	0.20 \pm 0.41 ^a	2.75 \pm 2.27 ^a	1.30 \pm 1.30 ^a	2.60 \pm 2.39 ^a
	<i>Corylus mandshurica</i>	2.40 \pm 2.82 ^b	2.45 \pm 3.44 ^a	0.25 \pm 0.44 ^a	3.15 \pm 2.30 ^a	0.40 \pm 0.82 ^b	1.35 \pm 1.14 ^b
	<i>Corylus heterophylla</i>	3.30 \pm 3.25 ^b	2.75 \pm 3.70 ^a	0.10 \pm 0.31 ^a	2.70 \pm 2.30 ^a	0.10 \pm 0.31 ^c	1.05 \pm 0.94 ^c
	<i>Juglans mandshurica</i>	6.45 \pm 3.68 ^b	0.05 \pm 0.22 ^c	0.40 \pm 0.82 ^a	0.50 \pm 1.00 ^b	0.35 \pm 0.59 ^b	2.25 \pm 2.38 ^a
	<i>Quercus mongolica</i>	1.10 \pm 1.45 ^a	3.85 \pm 4.12 ^b	0.15 \pm 0.37 ^a	3.95 \pm 2.72 ^c	0.00 \pm 0.00 ^c	1.00 \pm 1.49 ^c
Rodent species	<i>Apodemus peninsulae</i>	1.82 \pm 1.66 ^a	0.33 \pm 0.77 ^a	0.24 \pm 0.61 ^a	4.42 \pm 2.21 ^a	0.44 \pm 0.72 ^a	2.73 \pm 1.84 ^a
	<i>Tamias sibiricus</i>	2.09 \pm 4.02 ^a	5.97 \pm 3.39 ^b	0.11 \pm 0.32 ^a	1.00 \pm 0.94 ^b	0.66 \pm 1.16 ^a	0.20 \pm 0.41 ^b
	<i>Clethrionomys rufocanus</i>	6.45 \pm 2.46 ^b	0.10 \pm 0.31 ^a	0.35 \pm 0.49 ^a	1.40 \pm 2.00 ^b	0.00 \pm 0.00 ^b	1.80 \pm 1.80 ^a

Tab. 3 - Two-way ANOVA summary of seed fates correlated with seed and rodent species.

Seed Fates	Source	Sum of Squares	df	Mean Square	F value	P value
IS	Rodent species	327.169	2	163.585	166.928	< 0.001
	Seed species	390.573	4	97.643	99.639	< 0.001
EIS	Rodent species	742.469	2	371.234	487.364	< 0.001
	Seed species	122.558	4	30.639	40.224	< 0.001
IAR	Rodent species	0.756	2	0.378	1.813	0.169
	Seed species	0.353	4	0.088	0.424	0.791
EAR	Rodent species	270.262	2	135.131	104.642	< 0.001
	Seed species	114.278	4	28.570	22.124	< 0.001
SH	Rodent species	5.513	2	2.757	6.532	0.002
	Seed species	13.820	4	3.455	8.186	< 0.001
LH	Rodent species	126.600	2	63.300	46.032	< 0.001
	Seed species	48.490	4	12.123	8.816	< 0.001

Tab. 4 - Linear regression results between seed fates and seed traits. Seed fates in the table were defined as: intact *in situ* (IIS), eaten *in situ* (EIS); eaten after removal (EAR), intact after removal (on surface) (IAR), scatter-hoarded (SH) and larder-hoarded (LH).

Seed fates	Seed mass (g)	Seed coat thickness (cm)	Tannin content (%)	Caloric value per seed (KJ)	Caloric value (KJ/g)
IIS	$r = 0.867$	$r = 0.909$	$r = -0.427$	$r = 0.823$	$r = 0.644$
	$P = 0.057$	$P = 0.033$	$P = 0.462$	$P = 0.083$	$P = 0.241$
EIS	$r = -0.809$	$r = -0.827$	$r = 0.649$	$r = -0.792$	$r = -0.942$
	$P = 0.098$	$P = 0.084$	$P = 0.236$	$P = 0.110$	$P = 0.017$
IAR	$r = 0.829$	$r = 0.520$	$r = -0.335$	$r = 0.844$	$r = 0.850$
	$P = 0.083$	$P = 0.369$	$P = 0.582$	$P = 0.073$	$P = 0.068$
EAR	$r = -0.855$	$r = -0.905$	$r = 0.598$	$r = -0.823$	$r = -0.892$
	$P = 0.065$	$P = 0.035$	$P = 0.287$	$P = 0.083$	$P = 0.042$
SH	$r = -0.184$	$r = -0.067$	$r = -0.483$	$r = -0.158$	$r = 0.499$
	$P = 0.767$	$P = 0.915$	$P = 0.410$	$P = 0.800$	$P = 0.392$
LH	$r = 0.375$	$r = 0.317$	$r = -0.519$	$r = 0.396$	$r = 0.876$
	$P = 0.534$	$P = 0.603$	$P = 0.370$	$P = 0.509$	$P = 0.051$

phylla > *J. mandshurica* (Fig. 1A, Fig. 2A). As in *A. peninsulae*, also *T. sibiricus* showed significant differences in seed removal rates among the plant species (Wald = 19.01, df = 4, $P = 0.001$ - Fig. 1B, Fig. 2B). Finally, significant differences between plant species in seed removal rates were found in *C. rufocanus* (Wald = 20.73, df = 4, $P < 0.001$ - Fig. 1C), but with a different preference order: *Q. mongolica* > *P. koraiensis* > *C. mandshurica* > *C. heterophylla* > *J. mandshurica*.

Seed fates according to plant species

More seeds of *P. koraiensis* and *Q. mongolica* were removed from seed stations than those of *C. mandshurica*, *C. heterophylla* and *J. mandshurica* ($F = 99.639$, df = 4, $P < 0.001$ - Fig. 2, Tab. 2, Tab. 3). EIS and EAR seeds were significantly affected by seed species (EIS: $F = 40.224$, df = 4, $P < 0.001$; EAR: $F = 22.124$, df = 4, $P < 0.001$), with seeds of *Q. mongolica*, with the thinnest coat, showing the highest EIS and EAR rates (Tab. 2). Seeds of *P. koraiensis* were instead

more likely to be scatter-hoarded than the other four seed species ($F = 8.18$, df = 4, $P < 0.001$). Larder-hoarding was also affected by seed species, i.e., small rodents larder-hoarded more seeds of *P. koraiensis* and *J. mandshurica* than those of *Q. mongolica*, *C. mandshurica* and *C. heterophylla* (Fig. 2, Tab. 2, Tab. 3), indicating that seeds with high caloric value were more likely to be hoarded by rodents.

Seed fates according to rodent species

The three rodent species showed significantly different manipulations of seeds in term of total number of seeds remaining at seed stations ($F = 166.92$, df = 2, $P < 0.001$); more seeds were left by *C. rufocanus* than by *A. peninsulae* and *T. sibiricus*, respectively (all $P < 0.001$ - Fig. 2, Tab. 2, Tab. 3). *T. sibiricus*, with large body size, ate more seeds at seed stations than small-sized *A. peninsulae* and medium-sized *C. rufocanus* ($F = 487.36$, df = 2, $P < 0.001$). However, more seeds were eaten after removal (EAR) by *A. peninsulae* than by *C. rufocanus* and *T. sibiricus* ($F = 104.64$, df = 2, $P < 0.001$). *T. sibiricus* and *A. peninsulae* scatter-hoarded more seeds than *C. rufocanus* ($F = 6.53$, df = 2, $P < 0.001$). Finally, more seeds were larder-hoarded by *A. peninsulae* and *C. rufocanus* than by *T. sibiricus* ($F = 46.03$, df = 2, $P < 0.001$ - Fig. 2, Tab. 2, Tab. 3).

Correlation between seed traits and seed fates

Regression of the proportion of IIS vs. seed coat thickness indicated that seed species with thick coat were more likely to be left at seed stations ($r = 0.909$, $P < 0.05$ - Tab. 4). No significant relationship was found between the proportion of EIS and seed coat thickness ($r = -0.827$, $P = 0.084$); however, the proportion of EIS was negatively correlated with the caloric value of seeds ($r = -0.942$, $P < 0.05$). We also found that the proportion of EAR was negatively correlated with both coat thickness and caloric value of seeds ($r = -0.905$, $P < 0.05$; $r = -0.892$, $P < 0.05$, respectively). Seed caloric value was positively and marginally correlated with the

proportion of larder-hoarded seeds ($r = 0.876$, $P = 0.051$), but not with scatter-hoarded seeds ($r = 0.499$, $P > 0.05$).

Discussion

High level of defense (e.g., thick seed coat) to predators usually reduces seed removal rates from seed stations by seed dispersers (Zhang & Zhang 2008). Our results support the first prediction suggesting that thick-coated seeds are removed more slowly than thin-coated seeds by small rodents because they may require greater efforts to handle. Rodents have to spend more time to eat seeds with thick coat, which may increase predation risk (Howe 1979); selecting thin-coated seeds may reflect their feeding strategies. Previous studies suggest that large-sized seeds are more likely to be cached by rodents (Xiao et al. 2004, 2005a, 2006, Celis-Diez & Bustamante 2005). In the three investigated rodent species, we fail to detect any apparent relationship between seed mass/size and number of seeds eaten or hoarded. More *Q. mongolica* acorns, the richest in tannins, were eaten either *in situ* or after removal than those of the other four plant species, inconsistent with the high tannin hypothesis (Steele et al. 1993). This suggests that tannin contents in seeds are unimportant in determining seed hoarding by rodents in our study region (Zhang et al. 2013). Early germinating *Q. mongolica* acorns were eaten instantly rather than hoarded, in agreement with the perishability hypothesis (Hadj-Chikh et al. 1996, Steele et al. 2001, Xiao et al. 2013). We propose that in *Q. mongolica* instant consuming rather than acorn caching is probably related to their higher perishability (Smallwood et al. 2001, Goheen & Swihart 2003, Steele et al. 2006). A seed coat thinner than those of other seed species might be an alternative explanation for instant consumption of *Q. mongolica* acorns by small rodents. Therefore, the effect of seed mass and tannin on seed fates might be masked by other prominent seed traits, e.g., seed coat (Pons & Pausas 2007). The significant and negative correlations between seed removal rates and seed coat thickness reflect the crucial role of seed coat in determining seed selection and seed dispersal (Zhang & Zhang 2008).

No significant relationship was found between seed coat thickness and the proportion of EIS. Our second prediction that thick-coated seeds are less likely to be eaten *in situ* but more likely to be eaten after removal is not fully demonstrated in this study. Although feeding thick-coated seeds after moving them away would be a safer way to prevent rodents from predation risk (Howe 1979), our results show a significant and negative relationship between the proportion of EAR and seed coat thickness. These results indicate that seeds with extreme thick

coat (e.g., *J. mandshurica*) prevent small rodents to disperse and eat them, generally reflecting the negative effect of thick seed coat on seed dispersal (Zhang & Zhang 2008).

Also the prediction that seeds with high caloric value are more hoarded by rodents is verified in this study. Seeds of *P. koraiensis* and *J. mandshurica* with high caloric value were more likely to be larder-hoarded, but less likely to be eaten by small rodents, in agreement with previous observations reporting that small rodents prefer to cache seeds with high nutritional value (Forget et al. 1998, Garb et al. 2000, Brewer 2001, Finkelstein & Grubb 2002). The significant and positive relationship between the proportion of larder-hoarded seeds and the caloric value of seeds also indicates the important role of energy reserves in seeds in determining food hoarding by animals (Jansen et al. 2002). More seeds of *P. koraiensis* were scatter-hoarded than those of *J. mandshurica*, although the latter shows higher caloric value per seed, reflecting the trade-offs between nutrition rewards and efforts in handling the thick coat of *J. mandshurica* seeds.

Animals with different body size may display different seed disposal abilities, and therefore show different preferences for seeds with contrasting traits (Muñoz & Bonal 2008a, Zhang & Zhang 2008). In our study, the large *T. sibiricus* ate more seeds *in situ*, while the medium-small *A. peninsulae* and *C. rufocanus* ate more seeds after removing them to safe places (e.g., corners and nests), supporting our fourth prediction. Actually, body size cannot always indicate seed handling ability, as *T. sibiricus* refuse to select seeds of *J. mandshurica*.

Larder-hoarding animals usually store food in their nests and invest more efforts to defend them, while scatter-hoarders bury one or several seeds in dispersed caches and space them far apart (Jenkins et al. 1995). Although it has been suggested that scatter-hoarding is due to poor ability of animals defending food caches (MacDonald 1976, Preston & Jacobs 2001), *A. peninsulae* and *C. rufocanus*, with small body mass, larder-hoarded more seeds than *T. sibiricus* did, while *T. sibiricus* scatter-hoarded more seeds than *A. peninsulae* and *C. rufocanus*. Contrasting with the last prediction, our results suggest that body size is not linked with the evolution of food hoarding strategies (scatter-hoarding and larder-hoarding). Caching strategies may represent trade-offs between cache defense maximization and cache pilferage minimization (Hurly & Lourie 1997, Gerhardt 2005, Dally et al. 2006).

We acknowledge that many environmental factors may influence seed selection, seed removal and dispersal, and ultimately seed fates in the field (Hay & Fuller 1981, Holl & Lulow 1997, García-Castaño et al. 2006, Meng et al. 2012). Although the same-sized

enclosures have been applied to investigate caching behavior of chipmunks and other rodent species (Zhang et al. 2008, Chang et al. 2009, 2010, Huang et al. 2011), the semi-natural enclosures cannot completely mimic the field conditions. Lack of competition and unnatural presentation of seeds are supposed to alter the behavior of rodents in the enclosures. Although previous studies show that the average dispersal distances of seeds of *P. koraiensis*, *C. mandshurica*, *C. heterophylla*, and *J. mandshurica* are less than 4 m in the field (Yi et al. 2008, Yi & Zhang 2008, Yi & Yang 2010), the enclosures may not be large enough to allow the expression of rodents' desired seed dispersal range.

Our results shed light on the interaction and coevolution between rodents and plants bearing large seeds. On one hand, plants need to increase seed size and nutrition contents to attract potential dispersers. On the other hand, plants have to avoid predation through developing various physical and chemical defense systems (Steele et al. 1993, Zhang & Zhang 2008). Trade-offs between attractive and defensive traits of plants regulates dispersers' decision to remove, consume, and hoard seeds. From the animal's point of view, trade-offs between costs and rewards of manipulating seeds may shape their different abilities of handling, consuming, and hoarding a seed. Thus, the interactions between plant seeds and rodents are often complex and diffuse at community level. The combined effects of seeds and rodents appear to play an important role in determining seed dispersal and predation in the seed-rodent dispersal system.

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