

The effects of kernel mass and nutrition reward on seed dispersal of three tree species by small rodents

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Abstract In the present study, colored tags were fastened to individual seeds to investigate seed dispersal and seed fates of *Pinus koraiensis*, *Corylus mandshurica*, and *Corylus heterophylla* with different seed traits. Our aim was to determine the role of the proportion of kernel mass, caloric reward per seed, and tag color in affecting seed removal rates and seed fates. We predicted that higher proportion of kernel mass and caloric reward will favor seed removal and caching, while lower ones will facilitate seed consumption either in situ or after removal. Our results showed that the proportion of kernel mass, rather than seed size, played an important role in determining seed removal rates and seed fates. Seeds of *C. heterophylla* with the lowest proportion of kernel mass, regardless of their largest size and/or mass, had lower removal rates, lower level of caching but higher proportion of consumption in situ compared with *P. koraiensis* and *C. mandshurica* seeds. Seeds with higher caloric reward exhibited greater dispersal distances. Seed kernel proportion was closely correlated to seed removal rates and caching rates, while seed size and hull thickness seemed to play less important role in affecting seed dispersal, probably because the higher seed

handling ability of small rodents in the experimental areas. Our investigation revealed no significant effect of tag color on seed removal rates and seed fates of the three seed species.

Keywords Seed dispersal · Seed fate · Kernel mass · Caloric reward · Seed size · Seed mass · Colored tag marking

Introduction

During the long-term evolutionary process, plants have developed numerous seed dispersal adaptations that ensure successful distribution to other habitats far from parent trees. Some seeds are dispersed by wind, others by water or by animals, such as frugivorous birds or granivorous rodents (Herrera et al. 1994; Yi and Zhang 2008). Being too heavy to blow in wind or flow in water, seeds of large mass or size do not move far from the mother plants at maturity (Abe et al. 2006); thus, they rely on seed dispersal agents to transport seeds beyond the canopy. A great portion of propagules of plant species bearing large seeds can be dispersed away from parent trees for successful seedling establishment and regeneration by birds and mammals that eat or disperse their fruits or seeds (Vander Wall 1990; Herrera et al. 1994; Xiao et al. 2006a). In temperate and sub-tropical ecosystems, many vertebrate animals are predators and/or dispersers of seeds of particular plant species (Godoy and Jordano 2001; Kaplin and Lambert 2002; Wang and Smith 2002; Xiao et al. 2006a; Yi et al. 2008; Yi and Zhang 2008; Cao et al. 2011). Therefore, tracking the ultimate fates of dispersed seeds is important for evaluating dispersal effectiveness of plant species by animals (Levey and Sargent 2000; Wang and Smith 2002).

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Every seed-eating vertebrate will face the decision whether to consume or remove and where to cache seeds at their first encounter with the seeds based on evaluation of many factors: e.g., seed size/mass, nutrition contents, hull thickness, chemical defenses of seeds, seed crop size as well as dispersers' abundance (e.g., Shimada 2001; Vander Wall 2001; Jansen et al. 2004; Heredia and Detrain 2005; Moore et al. 2007; Zhang and Zhang 2008). Large seeds have been found to have higher predation probability but lower survivorship than small ones (e.g., Moles et al. 2003). However, several studies indicate the opposite pattern that large seeds are more likely to be removed and then cached, rather than eaten in situ both at inter- and intraspecific levels (Vander Wall 2003; Xiao et al. 2006a; Chang et al. 2009; Wang and Chen 2009). Seeds with higher nutrition contents are usually found to exhibit higher probability of being cached rather than consumed instantly (Xiao et al. 2003). Seed hull thickness has been recognized as another important factor influencing seed removal and caching; seeds with hard and thick hull tend to be removed and then cached than those with thin and soft ones (Lu and Zhang 2005; Zhang and Zhang 2008). However, there may not be a positive correlation between seed size, nutrition rewards, and seed hull thickness as the seed is a combination of seed hull, embryo, and endospermic tissue displaying differences in origin and development. Large seeds would be less selected and cached due to their thick seed hull and low proportion of kernel mass (nutrition rewards), and small seeds with higher proportion of kernel mass would less likely to be removed and cached (Yu et al. 2011). Therefore, effect of seed traits on seed dispersal patterns by small rodents is generally considered to be controversial and complicated at present (Brewer 2001; Wang and Smith 2002; Theimer 2003; Ulft 2004; Moore et al. 2007; Muñoz and Bonal 2008).

In addition, one of the biggest obstacles to study of seed dispersal is the difficulty of tracking seeds dispersed by animals in the field. Plastic tags have been widely used in dispersal ecology for retrieving dispersed seeds (Xiao et al. 2003, 2004, 2005a, b, 2006a, b; Yi and Zhang 2008; Yi et al. 2008, 2011). Although the plastic tags have proven to have neglectable influence on seed dispersal, it still remains unknown whether the tag color affects animal's selecting tagged seeds and whether dispersers would have color blindness, as the eyesight significantly differed between nocturnal and diurnal animals. To further understand the complex interactions between seed traits and seed dispersal, we examined seed dispersal of three sympatric large-seeded tree species (*Pinus koraiensis*, *Corylus mandshurica*, and *Corylus heterophylla*) with different seed properties in a north temperate forest in the Lesser Xing'an Mountain, China. Seeds in the study area were marked individually with colored plastic tags (white, blue, and red). The main

purpose of this study was to assess the effects of the proportion of kernel mass, caloric reward, seed size, and hull thickness on the rates of seed consumption, removal, and caching. We predicted that (1) seeds with higher kernel mass and caloric reward would have higher removal rates, (2) seeds with higher kernel mass and caloric reward are more likely to be removed and cached, (3) seeds with higher kernel mass and caloric reward would be dispersed at further distance, and (4) color of tags will not affect seed removal and seed fates of the investigated seed species. We also evaluated the effects of tagging on seed dispersal by small rodents.

Materials and methods

Study site

The study was conducted in September 2007 in the Dongfanghong Forestry Center (mean elevation of 750 m, 45°58'N, 129°08'E) in the Dailing District, Yichun City, Heilongjiang Province, northeast China. The climate at the site is dominated by the north temperate zonal monsoons with long, severe winters and short cool summers. The annual average air temperature is 1.4°C with a maximum of 37°C and minimum of -40°C. Average annual precipitation averages 650 mm, 80% of which falls between May and September. The zonal vegetation is characterized by secondary broad-leaf and mixed conifer forests. At our study sites, common canopy tree species include *Betula platyphlla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurese*, *Acer mono*, and *Tilia amurensis*; beneath the tree species, the dominant shrubs are *Corylus mandshurica*, *C. heterophylla*, *Fructus schisandrae*, *Acanthopanax senticosus*, etc.

The study was carried out in a uniform Mongolian oak-dominated secondary forest with an area of 5.3 km².

Seed traits

Experimental mature seeds of last autumn were obtained in the local market because they were economic food items. Thirty intact seeds of each seed species (*P. koraiensis*, *C. mandshurica*, and *C. heterophylla*) were selected randomly for measuring morphological and chemical traits. Seed mass and kernel mass of individual seeds were weighed with an electronic scale (measured to 0.01 g) after drying at 70–80°C for 24 h in a constant oven. Seed length, width, and hull thickness were measured with an electronic vernier caliper (measured to 0.01 mm). Concentrations of crude protein, crude fat, crude starch, and tannin of the seed species were measured by Cereal Quality Supervision and Testing Centre, Ministry of Agriculture, China (No. 12,

Southern Zhongguancun Road, Haidian District, Beijing). The caloric values of seeds were calculated by the average gross energy equivalents of protein (17.2 KJ/g), fat (38.9 KJ/g), and carbohydrates (17.2 KJ/g) (Yang 2002). Caloric value per seed was calculated using mean kernel mass \times caloric value and was used to reflect the nutritional value of the three seed species.

Field manipulations

In the experimental site, 60 seed stations (1 m \times 1 m in rectangular shape) were established 15–20 m apart along four 300-m-long transects. Sound seeds of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* were selected and labeled with different colored tags according to Yi and Zhang (2008) with minor modification. A hole, 0.3 mm in diameter, was drilled through the husk far from the embryo of each seed, without damaging the cotyledon and the embryo. A flexible plastic tag (2.5 cm \times 3.5 cm, <0.3 g) was tied through the hole in each seed using a thin 10-cm-long steel thread. Each colored tag was consecutively and discriminatively numbered to allow all seeds to be easily relocated and identified. When small rodents buried seeds in soil, shallow holes, or tree leaf litter, the colored tags were often left on the ground surface.

For the first 20 seed stations, each ten seeds of *P. koraiensis* marked with white, blue, and red color tag were placed at each seed station. Each ten seeds of *C. mandshurica* labeled with three different colored tags were released in the second 20 seed stations. The last 20 seed stations were established for releasing seeds of *C. heterophylla* with different color tags. Therefore, total 600 tagged seeds for each seed species were released in our experiment. We established additional three seed stations for each seed species and released 30 correspondent seeds without tagging, respectively. We compared the mean values of percent removal rates obtained from these three stations with those of the 20 stations for each seed species to evaluate the potential effect of tagging on seed removal rates. We checked the tagged seeds at each seed station every day for the first 13 days, and then we checked on the 16th and 23th day to investigate seed fates as described by Yi and Zhang (2008). The proximate fates of the released seeds were defined as intact in situ (IS), eaten in situ (EIS); eaten after removal (EAR), intact after removal (on surface) (IAR); cached after removal (in soil) (CAR); and missing (may be in burrow or not seen due to long-distance dispersal) (M).

Identification of small seed-dispersing mammals

To identify the potential dispersal agents in the study areas, we used live traps baited with one peanut to monitor small

rodent species and their relative abundances in autumn (late September) of 2007. Three transects were selected, 1,000 m from the seed stations, and 48 trap stations were set at 5-m intervals along each transect for two consecutive nights. The vegetation type of selected transects was the same as which the marked seeds were released. Three rodent species were trapped: *Apodemus peninsulae*, *Clethrionomys rufocanus*, and *Tamias sibiricus*. Additionally, the Eurasian jay *Garrulus glandarius* and *Sciurus vulgaris* are expected to play a less important role in participating in large-seed dispersal because we occasionally witnessed their activity. The low missing rates (2.33%) and short dispersal distances (4.11 \pm 2.40 m) of released seeds imply that released seeds were mainly removed by small rodents (Yi et al. 2008, this paper).

Data analyses

Cox regression was used to detect significant differences of seed removal rates for different seed species or color tagging. General linear model (GLM) was used to test differences of seed fates and the magnitudes of dispersal distances among the different tree species and color tagging. GLM was also applied to test the difference in seed traits. Spearman correlation was used to evaluate the relationship between dispersal measures and seed traits.

Results

Seed traits

Morphological and chemical traits of the three seed species were very different (Table 1). Seed size and mass were increasing with the order of *C. mandshurica*, *P. koraiensis*, and *C. heterophylla*. Seeds of *C. heterophylla* have a thicker hull than *P. koraiensis* and *C. mandshurica* ($F=84.031$, $df=2$, $P<0.001$). The caloric value of *C. heterophylla* was much lower than those of *C. mandshurica* and *P. koraiensis*, respectively ($F=2.001E3$, $df=2$, $P<0.001$) (Table 1). The effect of tannin as chemical defense can be neglected because its low concentration in the three seed species.

Effects of seed species

Our routine survey indicated that the seed removal rates differed significantly among the three tree species (Wald=16.348, $df=2$, $P<0.001$) (Fig. 1). Seed removal rate of *C. heterophylla* was significantly different from those of *P. koraiensis* (Wald=14.482, $df=1$, $P<0.001$) and *C. mandshurica*, respectively (Wald=8.337, $df=1$, $P<0.001$),

Table 1 Morphological and nutritional traits of the three seed species (mean±SD)

Seed traits	Seed species		
	<i>P. koraiensis</i>	<i>C. mandshurica</i>	<i>C. heterophylla</i>
Seed size (cm × cm) (n=30)	1.60×1.11	1.43×1.20	1.58×1.44
Seed mass (g) (n=30)	0.73±0.05	0.73±0.08	1.18±0.28
Thickness of seed hull (cm) (n=30)	0.11±0.01	0.11±0.01	0.24±0.03
The proportion of kernel mass (%) (n=30)	37.03±1.82	38.57±3.55	18.66±4.29
Tannin (%) ^a	0.02±0.01	0.25±0.02	0.07±0.01
Caloric value per seed (KJ) ^b	7.44±0.05	6.21±0.02	4.30±0.03

^a Thirty dry intact cleaned seeds of each species as a sample were used to measure tannin

^b Calculated based on the caloric value of crude fat, protein, and starch and their correspondent contents per seed

whereas no difference was found between the last two ($P > 0.05$). After 23 days, the proportion of removed seeds of *C. heterophylla* was 40 and 23 times lower than that of *P. koraiensis* and *C. mandshurica*, respectively.

As indicated in Fig. 2, small rodents showed a higher preference for seeds of *P. koraiensis* and *C. mandshurica* than *C. heterophylla* ($F = 26.701$, $df = 2$, $P < 0.001$). The proportion of IS of *C. heterophylla* was significantly higher

than those of *P. koraiensis* ($P = 0.001$) and *C. mandshurica* ($P = 0.001$), respectively, but there was no difference between *P. koraiensis* and *C. mandshurica* ($P = 0.707$). The proportion of IS was negatively correlated to the proportion of kernel mass (Table 2). The proportion of CAR was significantly different among the three tree species ($F = 8.211$, $df = 2$, $P = 0.001$), with *C. heterophylla* much lower than those of *P. koraiensis* and *C. mandshurica*

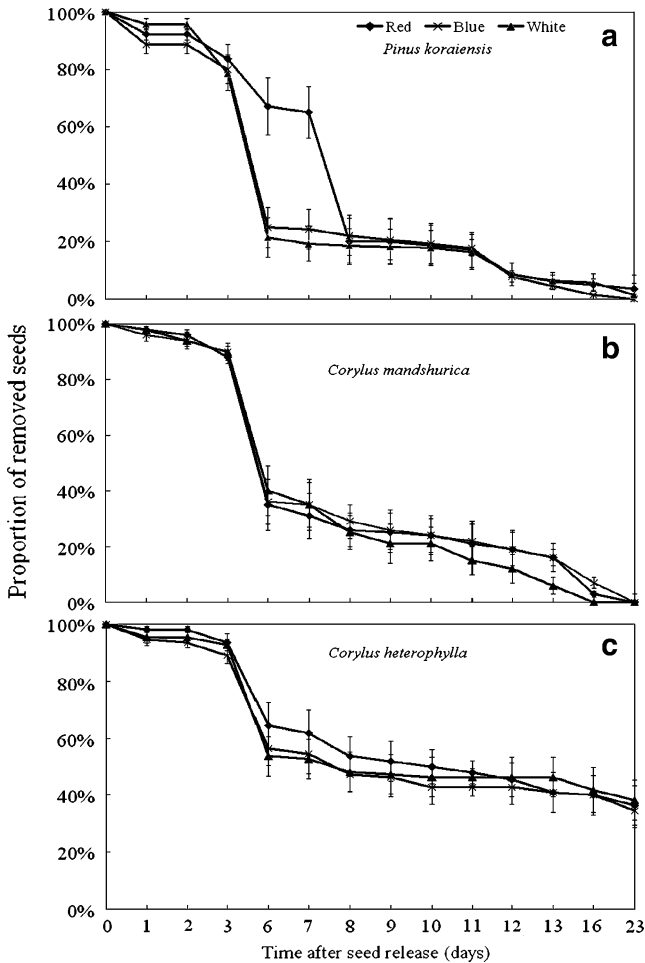


Fig. 1 Seed removal rates of *P. koraiensis* (a), *C. mandshurica* (b), and *C. heterophylla* (c) marked with plastic tags of three different colors after placing them in the field. X-axis has discontinuities, the same as below in Fig. 3. Data were expressed as mean±SD

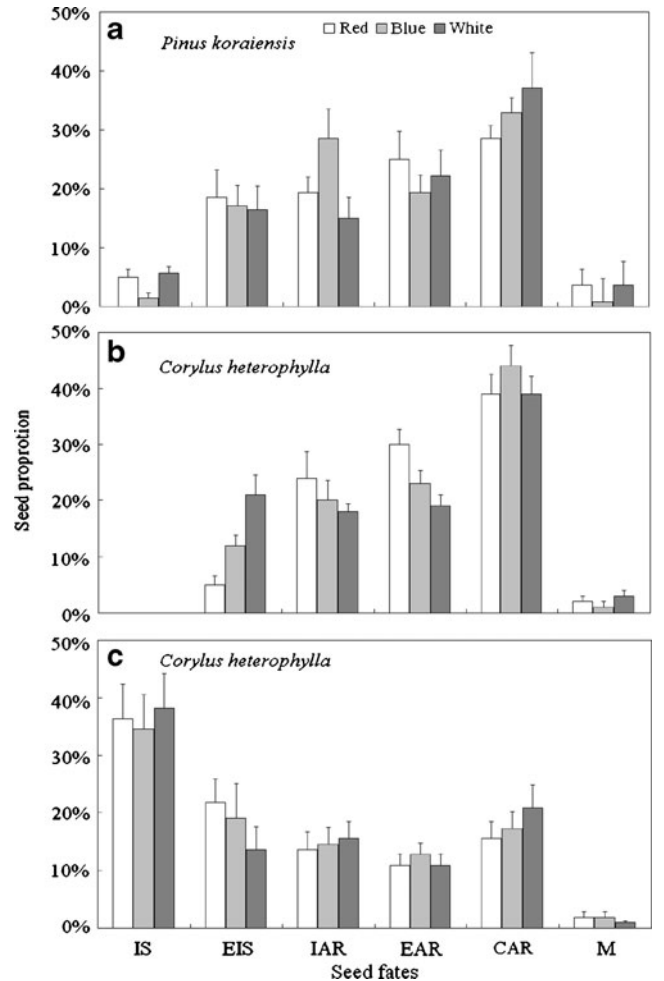


Fig. 2 Seed fates of *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* marked with different color tags after removal by small rodents. Data were expressed as mean±SD

Table 2 Correlation coefficients between dispersal measures and seed traits of the three seed species

Dispersal measures	Seed mass (g)	The proportion of kernel mass (%)	Caloric value per seed (KJ)	Seed hull thickness (cm)
IS	$r=-0.886$ $P=0.333$	$r=-1.000$ $P=0.000$	$r=-0.500$ $P=0.667$	$r=-0.886$ $P=0.333$
EIS	$r=0.886$ $P=0.333$	$r=-1.000$ $P=0.000$	$r=-0.500$ $P=0.667$	$r=0.886$ $P=0.333$
IAR	$r=-0.886$ $P=0.333$	$r=0.500$ $P=0.667$	$r=1.000$ $P=0.000$	$r=-0.886$ $P=0.333$
EAR	$r=-0.886$ $P=0.333$	$r=1.000$ $P=0.000$	$r=0.500$ $P=0.667$	$r=-0.886$ $P=0.333$
CAR	$r=-0.886$ $P=0.333$	$r=1.000$ $P=0.000$	$r=0.500$ $P=0.667$	$r=0.886$ $P=0.333$
Dispersal distance	$r=-0.886$ $P=0.333$	$r=0.500$ $P=0.667$	$r=1.000$ $P=0.000$	$r=-0.886$ $P=0.333$

IS intact in situ, EIS eaten in situ, IAR intact after removal, EAR eaten after removal, CAR cached after removal

($P=0.008$; $P<0.0001$). The proportion of CAR was positively correlated to the proportion of kernel mass (Table 2). The proportion of EAR and EIS were significantly different among the three seed species, respectively ($F=4.320$, $df=2$, $P=0.022$; $F=7.716$, $df=2$, $P=0.003$); the proportion of EAR of *C. heterophylla* was much lower than those of *P. koraiensis* and *C. mandshurica*, respectively ($P=0.056$; $P=0.004$). The proportion of EAR was positively correlated to the proportion of kernel mass (Table 2). The proportion of EIS of *C. heterophylla* was significantly higher than those of *P. koraiensis* and *C. mandshurica*, respectively ($P=0.007$; $P<0.001$) despite its thick seed hull. The proportion of EIS was negatively correlated to the proportion of kernel mass (Table 2). The proportion of IAR was positively correlated to the caloric value per seed (Table 2).

The mean dispersal distances of the three seed species were 2.49 m, 3.59 m, and 3.62 m for *C. heterophylla*, *C. mandshurica*, and *P. koraiensis*, respectively, and showed significant difference ($F=5.133$, $df=2$, $P=0.006$). The mean dispersal distance of *C. heterophylla* was remarkably lower than those of *P. koraiensis* and *C. mandshurica*, respectively (all $P=0.002$). The mean dispersal distances of *P. koraiensis* seeds with different fates (IAR, CAR, and EAR) were 4.38 m, 4.18 m, and 2.70 m, respectively ($F=3.109$, $df=2$, $P=0.046$); seeds cached were transported longer distances than those eaten after removal ($P=0.002$). The mean dispersal distances of *C. mandshurica* seeds with different fates (IAR, CAR, and EAR) were 2.47 m, 3.72 m, and 4.19 m, respectively ($F=6.777$, $df=2$, $P=0.001$); seeds cached or eaten after removal were transported longer distances than those remained intact after removal ($P=0.008$; $P=0.002$). However, the mean dispersal distances of *C. heterophylla* seeds with different fates (IAR, CAR, and

EAR) showed no difference ($F=0.693$, $df=2$, $P=0.502$). The average dispersal distance was positively correlated to the caloric value per seed (Table 2).

Differences among tag colors

Cox regression analyses demonstrated that colored tags showed minor effect on the seed removal rates of the three seed species investigated (Wald=2.023, $df=2$, $P=0.364$; Wald=2.102, $df=2$, $P=0.350$; Wald=6.007, $df=2$, $P=0.050$) (Fig. 1). Seeds without tags were removed at the same rate as tagged seeds for *P. koraiensis*, *C. mandshurica*, and *C. heterophylla*, respectively (Wald=3.489, $df=3$, $P=0.322$; Wald=3.278, $df=3$, $P=0.351$; Wald=7.470, $df=3$, $P=0.058$) (Fig. 3). Generally, the proportion of IS, EIS, IAR, EAR, CAR, and M labeled with colored tags was not significantly different in *P. koraiensis* (all $P>0.05$) (Fig. 2). Colored tags showed no significant influence on the seed fates of *C. mandshurica* and *C. heterophylla*, respectively

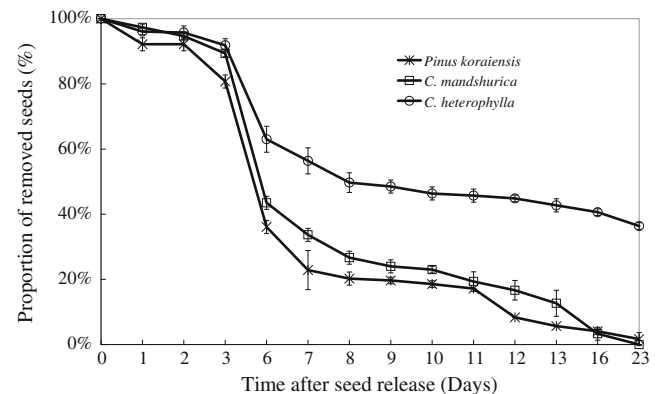


Fig. 3 Seed removal level of the three seeds species without tag marking released at seed stations. Data were expressed as mean±SD

(all $P > 0.05$) (Fig. 2). No effect of colored tag on the mean dispersal distance was detected in either of the three seed species (all $P > 0.05$).

Discussion

Our results showed significant differences in seed removal rates and the proportion of non-removed, consumed, and cached seeds among the three tree species but not among the three kinds of colored tags. Despite large size, seeds of *C. heterophylla* with the lowest kernel mass and caloric rewards were removed much slowly than the other two seed species, suggesting that the proportion of kernel mass and caloric reward per seed affect the seed removal rates by animals (Jansen and Forget 2001; Izhaki 2002; Xiao et al. 2006a; Zhang and Zhang 2008). Although our first prediction was well supported, the results failed to strengthen the previous studies showing that seeds with large size or mass are removed more quickly than those with small size or mass (Vander Wall 2003; Ulft 2004; Xiao et al. 2004, 2005a; Celis-Diez and Bustamante 2005; Xiao et al. 2006a), possibly because seeds with large size are also characterized by thick hull, lower kernel mass, and caloric rewards (Table 1), decreasing attractiveness of *C. heterophylla* seeds to small rodents.

Nutrient contents of seeds cached by animals, representing the trade-off between energy expenditure and acquisition, may also affect small rodents' final decision to dispose a given seed species (Kerley and Erasmus 1991; Alexander et al. 2001; Jansen and Forget 2001; Izhaki 2002; Xiao et al. 2006a; Zhang and Zhang 2008). Although handling and eating seeds with thick hull not only increases the energy expenditure required to open the seeds but also increases the predation risk on rodents (Kollmann et al. 1998), much more seeds of *C. heterophylla* were eaten in situ than the other two seed species with thin hull, indicating that seed hull thickness seems to play a less important role in affecting seed selection in our study (but see Zhang and Zhang 2008), probably because of the higher seed handling ability of small rodents. Less seeds of *C. heterophylla* were found to be cached by small rodents (Table 1), which can be explained by the fact that animals tend to cache seeds with higher nutrition rewards (Jansen and Forget 2001; Xiao et al. 2003). Heavier seeds with thick hull but less caloric rewards may be less attractive to small rodents to store. However, the lower proportion of CAR of *C. heterophylla* was not well in agreement with other results that large seeds are most likely to be removed and then hoarded (Vander Wall 2003; Xiao et al. 2006a, b). Furthermore, these results failed to support the prediction of Lu and Zhang (2005) that seeds with thick hull are more likely to be cached, possibly reflecting the negative role of

low nutrition rewards on seed caching of *C. heterophylla*. Therefore, the proportion of kernel mass as well as caloric reward per seed seems to play an important role in affecting seed caching due to the trade-off between energy investment and predation risk (Hurly and Robertson 1987), well supporting our second prediction.

Failing to support the suggestion that large seeds are most likely to be transported at further distance than small ones (Xiao et al. 2004, 2005a), we found seeds of *C. heterophylla* were dispersed in short distances compared with those of *P. koraiensis* and *C. mandshurica*. Jansen et al. (2004) propose that higher-value food items are usually transported and cached at greater distance, probably because pilferers are willing to expend more effort to find additional high-value items, which would well explain our results. Seeds of *P. koraiensis* and *C. mandshurica* with smaller size/mass were transported at further distances, further highlighting the role of proportion of kernel mass or caloric reward per seed in affecting seed dispersal measures (Table 2).

Although direct observations (Wenny and Levey 1998), magnets or small pieces of metal (Alverson and Díaz 1988; Steele et al. 2001), dispersal models (Murray 1988), genetic techniques (Dow and Ashley 1996), radioisotopic marking (Vander Wall 1994; Forget and Wenny 2005), fluorescent microspheres (Levey and Sargent 2000), stable isotope techniques (Hardesty et al. 2006; Paireon et al. 2006; Carlo et al. 2009), and radio-tracking method (Josep and Pausas 2007) have been used in seed dispersal ecology, thread and tag marking seems to be widely accepted in recent years (Zhang and Wang 2001; Hoshizaki and Hulme 2002; Li and Zhang 2003; Theimer 2003; Chauvet et al. 2004; Jansen et al. 2004; Xiao et al. 2005b; Yi and Zhang 2008). Our results on *P. koraiensis*, *C. mandshurica*, and *C. heterophylla* indicated that more than 90% of tagged seeds were successfully relocated at the end of the field experiments (Fig. 2), showing greater effectiveness and feasibility of tagging method for retrieving individual seeds than other tracking methods (Vander Wall 2002, 2003). In addition, seed dispersal patterns by small seed-dispersing rodents were similar to studies using other methods (Vander Wall 2002, 2003; Forget and Wenny 2005; Paireon et al. 2006), indicating little influence of tagging on animal behavior. Color tag marking of the dispersed seeds permits place-marking and following the seed fates in a non-invasive way, allowing a more accurate assessment of post-dispersal seed fates. We found no significant difference in seed removal rates and seed fates among the three kinds of colored tags for each seed species (Figs. 1 and 2), which provides insight into the foraging and seed-dispersal behavior of herbivorous animals in response to tag colors. Although nocturnal and diurnal animals may differ in

eyesight significantly, insensitivity to tag color in our study may indicate small rodents' color blindness (Coleman and Hamilton 1933), providing a solid basis for future tagging in seed dispersal studies. This approach can be widely extended to other large seeds and ecosystems. However, some caution is required that red, blue, and other colors such as yellow and green are easily camouflaged by leaf colors in the field, and so white tags are highly recommended for the researchers' ease.

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