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Pericarp thickness and seed size determine acorn dispersal of five rodent-dispersed oak species

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Abstract: Because the seed-eating and-hoarding behaviors of animals are complicated by seed traits，the relationships between seed traits and seed dispersal in animal-dispersed plants are still contentious and need further study. Here，we examined acorn dispersal，both in the field and in enclosure，of five rodent-dispersed oak species（*Quercus mongolica*，*Q. serrata var. brevipetiolata*，*Q. aliena*，*Q. variabilis* and *Q. liaotungensis*）with different morphological and chemical traits，to further explore the complex interactions between seed traits and seed dispersal. The results of the field studies showed that acorns with large size and thick pericarp were more likely to be cached than eaten by small rodents，suggesting the importance of seed mass and seed coat thickness in determining seed dispersal at the community level of rodents. Large size and thick pericarp acorns were dispersed further in the field，supporting previous studies that seed dispersal distances are positively correlated with seed mass and seed coat thickness. However，in the enclosures，only pericarp thickness of acorns consistently influenced seed removal，dispersal，and caching by *Tamias sibiricus* at the population level. Our studies indicate that the effect of seed traits on seed dispersal can be different at population and community levels，and therefore some caution is required in elucidating rodent-mediated seed dispersal measures.
Key words: Acorns；Pericarp thickness；Rodent；Seed dispersal；Seed size/mass

外果皮厚度和种子大小对五种栎属橡子扩散的影响

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摘要： 动物对种子的扩散和贮藏是一个复杂的生态学过程，常常受到种子特征的影响。有关种子特征如何影响动物对种子扩散，许多研究结果并非完全一致。我们于 2009 年 9 月在黑龙江东方红林场野外和围栏内释放五种栎属橡子（*Quercus mongolica*，*Q. serrata var. brevipetiolata*，*Q. aliena*，*Q. variabilis* 和 *Q. liaotungensis*），研究种子特征对鼠类（*Apodemus peninsulae*，*Clethrionomys rufocanus* 和 *Tamias sibiricus*）扩散和埋藏橡子的影响。野外释放结果表明：橡子大小和外果皮厚度显著影响鼠类对橡子的扩散和埋藏。鼠类偏向扩散和埋藏种皮厚的大橡子，种皮薄的小橡子则多被原地取食。种皮厚的大橡子扩散距离显著高于种皮薄的小橡子。然而，只有外果皮的厚度显著影响围栏内花鼠对橡子的扩散和埋藏，橡子大小并非主要的影响因素。种子特征影响种子扩散的效应可能在种群和群落水平上存在差异。
关键词： 鼠类；外果皮厚度；橡子；种子大小；种子扩散
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1 Introduction

Seed dispersal has been recognized as an important ecological interaction between food-hoarding animals and plants bearing large seeds（Vander Wall，1990；Schupp and Fuentes 1995；Terborgh *et al.*，2002，2008）. Various studies have shown that seed dispersal and caching by hoarding animals have significant impacts on seedling establishment，consequently affecting regeneration and spatial distribution，as well as long-term stability of populations of plants（Peres and Baider，1997；Vander Wall，2001；Sun *et al.*，2004；Siepielski and Benkman，2007，2008）. Many studies in various ecosystems have identified small rodents as very important seed dispersers and predators（Hulme，2002；Vander Wall and Longland，2004；

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Roth and Vander Wall, 2005), and their foraging behavior in response to different seed traits is a key predictor of the probability of seed survival (Moles *et al.*, 2003; Vander Wall, 2003; Xiao *et al.*, 2004; Wang and Chen, 2009).

Seed traits directly affect the eating and caching preferences of food hoarders during seed dispersal processes (Xiao *et al.*, 2004; Muňoz and Bonal, 2008; Zhang and Zhang, 2008; Wang and Chen, 2009), and these preferences may ultimately determine the seed fates and outcomes of plant fitness (e.g., Brewer, 2001; Vander Wall, 2001; Chauvet *et al.*, 2004; Kelt *et al.*, 2004; Sun *et al.*, 2004). Plant species can be different in various seed traits, e.g., seed size/mass, nutrient content, and physical (e.g. seed hull thickness) and chemical (e.g. tannins) defenses of seeds (Jensen, 1985; Kollman *et al.*, 1998; Moles *et al.*, 2003; Zhang and Zhang, 2008). Since the interaction between seeds and rodents influences plant fitness, understanding how seed traits affect rodent feeding and caching behavior is of great importance (Hadj-Chikh, 2003). Although previous studies have largely focused on how seed traits affect the probability that seeds are selected and cached by hoarders (Briones-Salas *et al.*, 2006; Muňoz and Bonal, 2008; Zhang *et al.*, 2005, 2008), how seed traits influence foraging and caching behaviors of rodents still remains unclear and controversial (Forget *et al.*, 1998; Moles *et al.*, 2003; Vander Wall, 2003; Xiao *et al.*, 2003, 2004, 2006; Zhang and Zhang, 2008; Takechi *et al.*, 2009; Wang and Chen, 2009; Yu *et al.*, 2011). Moreover, there is always an integrated effect of several seed traits on seed dispersal by animals (Brewer, 2001; Shimada, 2001; Jansen *et al.*, 2002; Heredia and Detrain, 2005), especially when seed species of different genera were tested (Zhang and Zhang, 2008; Yu *et al.*, 2011).

In addition, Muňoz and Bonal (2008) proposed that rodent species with larger body size will exhibit higher ability to handle large-sized seeds. Large-bodied rodent species are expected to forage seed species across a wider range of seed sizes than do those with small body sizes. Small rodents may also possess different capabilities to cope with chemical defenses of seeds (Kenward and Holm, 1993; Saitoh *et al.*, 2007). In this context, seed dispersal patterns can be different at the population and community levels in response to the same food sources, as different rodent species co-occurring in the field respond differently to a given seed trait. However, little is known about how seed traits affect seed choice by rodents at the population and community levels.

In the present study, we examined acorn dispersal of five rodent-dispersed oak species (*Quercus mongolica*, *Q. serrata var. brevipetiolata*, *Q. aliena*, *Q. variabilis* and *Q. liaotungensis*, hereafter QM, QS, QA, QV, and QL) with different seed traits in north temperate forests, China, to isolate the key factors determining seed removal and seed fates. The purpose of this study was to assess the effect of acorn size/mass, pericarp thickness, and chemical traits on acorn removal, consumption and scatter-hoarding by small rodents. Because food hoarding animals will gain more energy rewards from larger acorns (Wang and Chen, 2009), we predicted that large acorns would be removed more quickly than small ones. Rodents would be exposed to higher risks of predation if they spend more time to eat large and/or hoard seeds in situ (Zhang and Zhang, 2008). We, therefore, predicted that large and/or hard acorns (with thick pericarp) would have lower proportion of consumption in situ, higher proportions of removal and scatter-hoarding than small and/or soft acorns. Specifically, we assessed whether there was any difference in seed dispersal patterns by small rodents at the population and community levels, in terms of seed removal, eating, and caching.

2 Materials and methods

2.1 Study site

The study was conducted in late September 2009 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℃ with a maximum of 37℃ and minimum of −40℃. Average annual precipitation is 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*. The dominant shrubs are *Corylus mandshurica*, *C. heterophylla*, *Fructus schisandrae* and *Acanthopanax senticosus* (Yi *et al.*, 2011a).

Small rodent species (*Apodemus peninsulae*, *Clethrionomys rufocanus*, and *Tamias sibiricus*) actively participate in acorn dispersal (Yi *et al.*, 2011b). *Tamias sibiricus* (104.8±9.3 g, n=7, Mean±SD) are larger than *A. peninsulae* (26.8±5.6 g, n=9) and *C. rufocanus* (33.4±3.6 g, n=7). In addition, the Eurasian jay (*Garrulus glandarius*) also consumed and dispersed these acorns, but may play a quantitatively less important role in seed dispersal because they are rarely witnessed in the study area (Yi's observation).

2.2 Acorn tagging and placement

2.2.1 Acorn collection

There was a relatively good seed crop of QM in 2009 in the study area, so we collected their acorns for experiments from 30 trees using seed traps. Acorns of QS, QA, and QV oak species were collected from 24 trees using seed traps in Henan Province, central China. Acorns of QL were collected from more than 20 trees in Liaoning Province, Northeastern China. Therefore, acorns of each oak species represent a composite sample.

2.2.2 Experiment plot for seed placement

The experiment was conducted at the end period of seed rain of QM (late September 2009). A total of 120 seed stations were spaced at 20-30 m apart in 12 parallel transect lines 200-300 m long at the experimental sites. Sound acorns of five oak tree species were selected and labeled using methods by Zhang and Wang (2001) with modification. Field study has shown that small rodents usually bury the tagged acorns in the soil or under tree leaves, while leaving the tags on the ground surface, making them easy to be re-located (Yi *et al.*, 2011a). Tagging has proven to have a negligible effect on seed removal and caching by small rodents in our previous studies (Yi *et al.*, 2011a). Thirty acorns were randomly selected for each oak species to incorporate intra-specific variations for measurement of seed length, seed width and fresh mass. Twenty acorns of each oak species were assigned for pericarp thickness measurement. Crude protein, crude fat, crude starch and tannins of the acorns were measured by the Cereal Quality Supervision and Testing Centre, Ministry of Agriculture, China (No. 12, Southern Zhongguancun Road, Haidian District, Beijing). Six samples each containing 30 acorns were analyzed for each oak species. The caloric values of acorns 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). Caloric value per acorn was calculated using mean kernel mass×caloric value (also see Zhang and Zhang, 2008). There were significant differences in acorn size/mass, pericarp thickness and caloric value among the five oak species (see Table 1).

Table 1 Seed traits of the five oak species (Mean±SD) and their correlation with seed fates

	Length (mm) (n=30)	Maximum width (mm) (n=30)	Fresh mass (g) (n=30)	Caloric value per acorn (kJ) (n=6)	Pericarp thickness (mm) (n=20)
QV	21.69±2.06^{a}	17.68±1.70^{a}	4.30±0.82^{a}	46.79±2.05^{a}	0.65±0.05^{a}
QA	22.10±1.84^{a}	14.80±1.40^{b}	2.97±0.68^{c}	29.81±1.80^{b}	0.43±0.05^{c}
QS	15.21±1.73^{c}	11.26±0.73^{c}	1.12±0.24^{e}	10.01±0.18^{d}	0.21±0.05^{d}
QM	21.33±2.13^{a}	17.00±1.62^{a}	3.64±1.13^{b}	27.59±4.33^{b}	0.52±0.18^{b}
QL	17.40±2.32^{b}	14.51±1.00^{b}	2.14±0.60^{d}	17.73±1.77^{c}	0.47±0.05^{b}
CAR (in the field)	r=0.710	r=0.939*	r=0.882*	r=0.837	r=0.944*
EIS (in the field)	r=-0.760	r=-0.952*	r=-0.901*	r=-0.847	r=-0.994*
Dispersal distance	r=0.754	r=0.968*	r=0.932*	r=0.886*	r=0.999*
IS (in the enclosure)	r=0.457	r=0.853	r=0.726	r=0.595	r=0.892*
CAR (in the enclosure)	r=0.509	r=0.827	r=0.722	r=0.676	r=0.927*
EIS (in the enclosure)	r=-0.391	r=-0.801	r=-0.665	r=-0.559	r=-0.872*

Thirty intact seeds of each species were dried and treated as a sample to measure caloric values. The superscript * and different letters in the same column indicate significant difference, at P<0.05, while data sharing the same letter do not differ significantly at P=0.05. See abbreviations in the text

In each seed station (1.0 m^2), ten tagged acorns of each oak species were placed on the ground. A total of 1 200 acorns were released for each oak species. During the 4 consecutive days after seed placement, we checked the tagged acorns around each seed station to investigate acorn fates. We searched for tagged acorns or their fragments around each seed stations (radius ≈ 15 m) for twenty minutes. Seed fates were then defined as: intact in situ (IS), eaten in situ (EIS); eaten after removal (EAR), intact after removal (IAR);

cached after removal (CAR); missing (M). The scatter-hoarded acorns were rechecked 20 days after seed placement, and seedlings from the cached acorns were surveyed in June 2010.

2.3 Data analysis

The sample sizes were the same for the five oak species; therefore, One-way ANOVA was applied to test the differences in acorn length, width, fresh weight, caloric values and pericarp thickness among the five oak species. Cox regression was used to see differences in acorn removal rates among the five oak species. Nonparametric Tests K Related Samples (Friedman Test) was used to test the difference in the proportion of acorns eaten in situ or cached and cache survival rates after arc-sin transformation to obtain normality (Xiao *et al.*, 2006). The General linear model (LSD or SNK) procedure was used to compare the differences in the dispersal distances among oak species. Linear regression was used to detect the correlation between seed dispersal measures and acorn characteristics.

3 Results

3.1 Seed trait

One-way ANOVA analyses showed that morphological traits of acorns of the five oak species differed significantly (length: $F_{4,145} = 68.923$, $P < 0.001$; width: $F_{4,145} = 105.849$, $P < 0.001$, fresh mass: $F_{4,145} = 83.832$, $P < 0.001$; pericarp thickness: $F_{4,95} = 122.899$, $P < 0.001$) (Table 1). Significant differences were also detected in the caloric value per acorn of the five oak species (length: $F_{4,25} = 372.795$, $P < 0.001$) (Table 1).

3.2 Acorn removal and seed fates

In the field, nearly all acorns were harvested by small rodents by the fourth day after seed placement. No difference was found in the acorn removal rates among the five oak species ($\chi^2 = 0.379$, $df = 4$, $P = 0.984$) (Fig. 1). However, the proportion of EIS was significantly different among the five oak species ($\chi^2 = 239.404$, $df = 4$, $P < 0.001$) (Fig. 2). The proportion of EIS of QV was significantly lower than that of the other four oak species (all $P < 0.05$), while more acorns of QS were eaten in situ than the other oak species (all $P < 0.05$). Linear regression analyses indicated that the proportions of EIS of the five oak species were negatively correlated with acorn mass, acorn width, and pericarp thickness (Table 1). Our results indicated significant difference in the proportions of CAR among the five oak species ($\chi^2 = 182.142$, $df = 4$, $P < 0.001$) (Fig. 2). Many more acorns of QV were scatter-hoarded than were those of the other four oak species, while the proportion of CAR of QS was significantly lower than those of the other four oak species (all $P < 0.05$). Linear regression analyses revealed that the proportion of CAR of the five oak species was positively correlated with acorn mass, acorn width and pericarp thickness (Table 1). Our final survey demonstrated that the survival rates of the five oak species were significantly different ($\chi^2 = 124.382$, $df = 4$, $P < 0.001$), with QV (2.42%) much higher than the other four oak species, QA (0.98%), QS (0.18%), QM (1.62%), and QM (1.24%), respectively. No seedling of the five oak species was found in 2010.

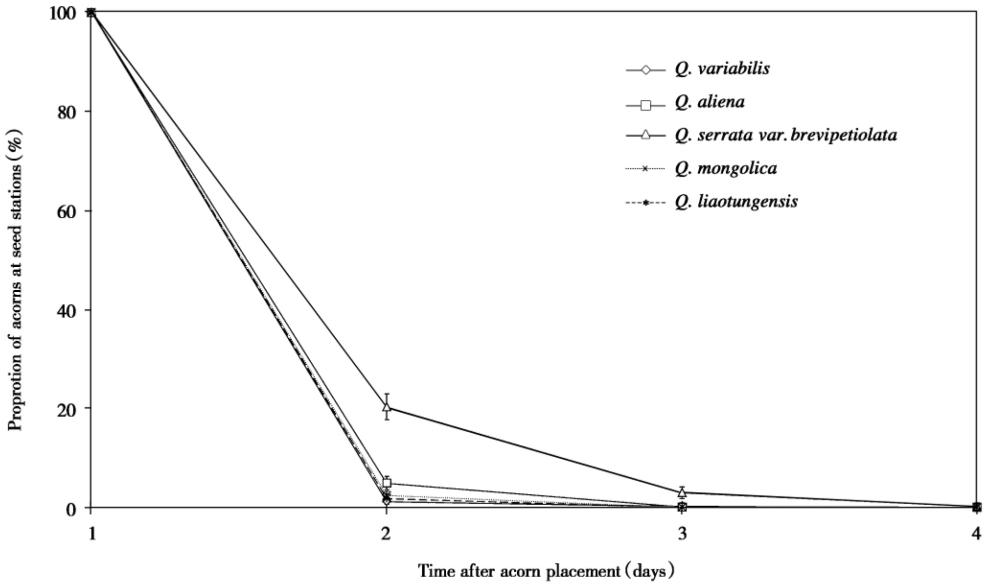

Fig. 1 Acorn harvest by small rodents in the field (Mean±SE)

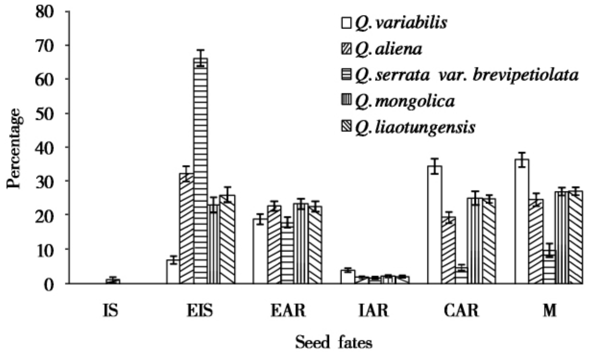

Fig. 2　Seed fate of the five oak species handled by small rodents in the field. See abbreviations in the text. Data are expressed as Mean±SE

In the enclosures, the proportion of acorns that remained at the seed stations (IS) was different among the five oak species when manipulated by Siberian chipmunks at the population level ($\chi^2 = 10.691$, $df = 4$, $P = 0.030$), and positively correlated with the pericarp thickness (Fig. 3, Table1). The proportions of EIS were significantly different among the five oak species but were negatively correlated with the pericarp thickness ($\chi^2 = 25.362$, $df = 4$, $P < 0.001$) (Fig. 3, Table1). The proportions of CAR of the five oak species varied greatly ($\chi^2 = 16.000$, $df = 4$, $P = 0.003$), and were also significantly correlated with the pericarp thickness (Fig. 3, Table 1).

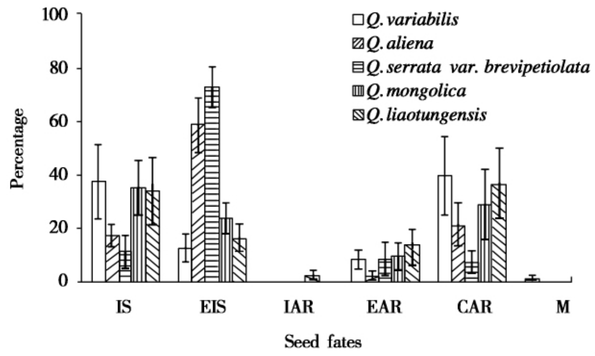

Fig. 3　Seed fate of the five oak species handled by Siberian chipmunks in the enclosures. Data are expressed as Mean±SE. See abbreviations in the text

3.3　Dispersal distances

The average dispersal distances were 6.86 ±0.18 m (Mean ± SE), 5.77 ± 0.18 m, 4.80 ±0.24 m, 6.23±0.17 m, and 5.96±0.18 m for QV, QA, QS, QM, and QL respectively, and varied significantly among the five oak species ($F_{4,2662} = 12.991$, $P < 0.001$) (Fig. 4). Acorns of QV were dispersed greater distances than those of other oak species. The average dispersal distance of QS acorns was much lower than those of QA, QM and QL respectively (Fig. 4). Linear analyses showed that the average seed dispersal distances of the five oak species were positively correlated with acorn mass, acorn width, pericarp thickness and caloric value, respectively (Table 1).

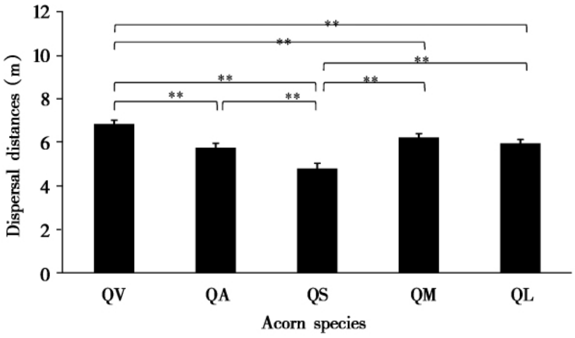

Fig. 4　Average dispersal distances of the five acorn species manipulated by small rodents in the field. Data are expressed as Mean ± SE. ** on the histograms indicates significant differences, $P < 0.01$

4 Discussion

No difference was found in acorn removal rates among the five oak species in the field, possibly due to the high level of rodent abundance at the end of seed fall of local tree species, *Q. mongolica*. Although more acorns with thick pericarps remained at the seed stations in the enclosures, no significant relationships were found between seed removal rates and acorn size/mass, failing to support previous studies that seed size affects seed dispersal at intra- and inter-specific levels (Vander Wall, 1990; Steele *et al.*, 1996; Brewer, 2001; Xiao *et al.*, 2004; Caccia *et al.*, 2006; Muňoz and Bonal, 2008). However, the significant and negative correlation between acorn removal rates and pericarp thickness was well in agreement with the results of Zhang and Zhang (2008) that seeds with hard hulls are less likely to be removed from seed stations. In this context, pericarp thickness seemed to be more important than other seed traits (e. g., seed size) in determining seed removal.

Eating larger acorns in situ not only increases the energy expenditure and time consumption but also increases predation risk (Xiao *et al.*, 2004). Our field results showed that the proportion of EIS was negatively correlated with acorn mass, implying the effect of seed mass on seed fates (Xiao *et al.*, 2004; Caccia *et al.*, 2006). Furthermore, we detected a negative relationship between pericarp thickness and seed consumption at the seed stations, well in agreement with previous studies (Hadj-Chikh *et al.*, 1996; Blate *et al.*, 1998; Zhang and Zhang, 2008). This can be explained by the close correlation between acorn mass and pericarp thickness. Handling and eating acorns with thick pericarps not only increases the energy expenditure required to carry or eat the seeds but also increases predation risk. Similarly, the proportion of CAR of the five oak species was positively correlated with acorn mass and pericarp thickness, indicating that small rodents tend to transport hard-to-handle acorns to safe areas for caching for later use. However, for Siberian chipmunks at the population level, the effects of acorn size/mass on caching activity were depressed, supporting the seed-hull enhanced dispersal hypothesis (Zhang and Zhang, 2008). Seed size/mass might not be an obstacle for chipmunks with larger body size to consume or disperse, compared with small wood mice. Despite close correlation between acorn mass and pericarp thickness, only pericarp thickness seems to exhibit consistent influences on acorn dispersal and caching in the field and enclosure experiments.

The correlation between dispersal distance and acorn mass supports the previous investigations that dispersal distance generally increases with seed size within a tree species and among different plant species (Vander Wall, 1995; Forget *et al.*, 1998; Jansen *et al.*, 2002; Xiao *et al.*, 2004). Although there were significant differences in acorn length and width between the five oak species, dispersal measures were constantly correlated with acorn width rather than length (Table 1), suggesting that animals may handle acorns based on their specific geometry (Steele *et al.*, 1993; Hadj-Chikh, 2003). Wider or round seeds are expected to evolve under selective predation by small rodents, as a strong selection for acorn characteristics has been observed in the mutual relationship between dispersers and oak species (Scarlett and Smith, 1991; Moore and Swihart, 2006).

Our studies indicate that both acorn mass and pericarp thickness play essential roles in determining seed removal and seed caching at the community level. However, for Siberian chipmunks at the population level, pericarp thickness becomes the prominent influence on acorn dispersal measures of the five oak species. These results suggest that rodent composition would regulate the way that seed traits affect seed dispersal. Seed dispersal measures can be manipulated by both seed traits and disperser agents. Although we obtained consolidated results from field investigations, our enclosure studies only focused on the caching behavior of Siberian chipmunks at the population level. Future studies on *Apodemus peninsulae* or *Clethrionomys rufocanus* at the population level are needed and expected to clearly show how rodent composition interferes with seed traits to affect seed dispersal.

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