Acorn Pericarp Removal as a Cache Management Strategy of the Siberian Chipmunk, *Tamias sibiricus*

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Abstract

Numerous recent studies have revealed a variety of behavioral adaptations of rodents for maximizing returns from cached seeds. Herein we report on a novel behavior by the Siberian chipmunk (*Tamias sibiricus*) in northeastern China, by which they consistently remove the pericarp (shell) of *Quercus mongolica* acorns before dispersing and caching these nuts. We investigated the effects of pericarp removal on acorn germination, tannin concentrations, cache pilferage, and insect damage, to determine if and how pericarp removal facilitates cache management by Siberian chipmunks and whether or not such behavior influences seed fates. Chipmunks cached acorns only after the pericarps were removed. Chipmunks preferred pericarp-removed acorns over intact acorns when removing them from seed stations for both consumption and caching. Pericarp removal did not affect germination or tannin concentration of cached *Q. mongolica* acorns, suggesting that the behavior is not an adaptation for long-term storage and tannin decomposition. Acetone treatments of the pericarp and artificial pericarp removal failed to alter pilferage rates by Siberian chipmunks and wood mice (*Apodemus peninsulae*). Since damage of acorns by weevils often leads to cache losses, we also tested the effects of weevil infestation on cache decision following pericarp removal. Siberian chipmunks removed pericarps and then scatter hoarded significantly more sound than weevil-infested acorns, strongly suggesting that pericarp removal is used to discriminate between the infested and non-infested acorns. Thus, we argue that the primary function of this behavior is to ensure successful storage of sound acorns, at least for short-term storage. Future studies should consider the potential impact of pericarp removal on weevil populations and long-term patterns of seed survival and establishment from the Siberian chipmunk's caches.

Introduction

Small mammals, because of their granivorous habits and scatter-hoarding behavior, often play an important role in the dispersal of large-seeded trees (Vander Wall 1990), and in early-stage mortality due to seed or seedling predation (Crawley 2000; Kitajima & Fenner 2000; Hulme & Benkman 2002). Hoarding animals rely on seeds as food supplies for survival and reproductive success (Smith & Reichmanm 1984; Vander Wall 1990). However, several studies have shown that intense management of caches is

necessary during the food-storing period to reduce cache losses to pilferers (Reichman 1988; Jansen et al. 2010; Steele et al. 2008), bacteria and fungi (Gendron & Reichman 1995; Emery et al. 2004), insect infestation (Steele et al. 1996), and perishability due to early germination (Fox 1982; Hadj-Chikh et al. 1996; Steele et al. 2001a; Jansen et al. 2006; Xiao et al. 2009).

Rodents appear to manage food stores by either selecting seeds that store better than others (e.g., those that are dormant, sound, less perishable, or higher in specific defense compounds) or by manipulating seeds (i.e., removing embryos) to alter their germination patterns and therefore storability (Reichman 1988; Steele et al. 1996, 2001b; Jansen et al. 2006; Xiao et al. 2009). The seeds of some tree species (e.g., white oaks, *Quercus*; section *Quercus*) are non-dormant and germinate in autumn immediately after seed fall (rather than after delayed dormancy) and quickly lose value once their energy stores are transferred into indigestible taproots (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001b, 2006; Goheen & Swihart 2003). Some rodents prune radicles to alter the perishability of seeds (Jansen et al. 2006; Cao et al. 2011; Yang et al. 2011), whereas others including at least two species of Asian squirrels (Pere David's rock squirrel, *Sciurotamias davidianus*; and Pallas' squirrel, *Callosciurus erythraeus*) (Xiao et al. 2009, 2010), and three species of North American tree squirrels [*Sciurus carolinensis, S. niger, S. aureogaster* (Fox 1982; Hadj-Chikh et al. 1996; Steele et al. 2001b, 2007)] have evolved the behavioral strategy of embryo excision to arrest seed germination and rapidly modify germinating seeds into long-term food reserves.

In the present study, we investigated a novel behavior by the Siberian chipmunk (*Tamias sibiricus*), in which the species nearly always removes the pericarp (shell) of acorns of *Quercus mongolica* prior to caching them (Yang et al. 2011). Herein, we sought to investigate whether and how pericarp removal behavior is related to cache management by Siberian chipmunks. We tested the following hypotheses that pericarp removal (1) accelerates desiccation of acorns and stops or at least postpones germination of acorns of *Q. mongolica*, thereby reducing seed perishability in caches; (2) prevents pilferage or facilitates cache recovery, by either preventing or enhancing olfactory cues that are present in the pericarp or cotyledons; (3) causes rapid leaching or decomposition of tannins in acorns; and (4) allows the Siberian chipmunk to discriminate between sound and insect-infested acorns for scatter hoarding, as infestation by

weevils (*Curculio* spp.) often leads to higher seed perishability.

Materials and Methods

Study Site and Species

The study was conducted in Sep 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 (Yi & Zhang 2008a). Acorns of Mongolian oak are dispersed and consumed by small rodents (*Apodemus peninsulae*, *Clethrionomys rufocanus*, *Tamias sibiricus*, and *Sciurus vulgaris*) and some birds (*Garrulus glandarius*) common to these forests. *Apodemus peninsulae* both scatterhoard and larderhoard seeds, whereas *C. rufocanus* act as larderhoarder only (XF Yi, unpublished data). Siberian chipmunks *Tamias sibiricus*, eat, disperse, and scatterhoard seeds of several local tree species (Yi & Zhang 2008a). However, *Sciurus vulgaris* and *Garrulus glandarius* are not common at the study area. Siberian chipmunks in this study were captured with steel-framed live-traps (9 cm × 10 cm × 25 cm) and maintained individually in steel-framed cages (90 cm × 40 cm × 50 cm) at room temperature and a natural photoperiod (14:10, L:D cycle). A total of 16 healthy adult Siberian chipmunks were used for behavioral experiments in semi-natural enclosures (see below) after 1 wk of acclimation to captivity. Prior to each experimental trial, plastic-tagged acorns were placed into the seed stations for animals to consume or scatter hoard. Acorns were labeled using methods slightly modified from those reported by Yi & Zhang (2008a). A minute hole (0.3 mm in diameter) was drilled at the basal end of each acorn, avoiding any damage to the embryo. We slipped a 10-cm thin steel wire through the hole and fastened it to the acorn, and then fastened a white flexible plastic tag (2.5 cm × 3.5 cm, <0.3 g) to the opposite end of the steel thread.

Experimental Protocols

We conducted behavioral experiments in 16 separate semi-natural enclosures (10 m × 10 m) previously established in an open, non-forested area (Fig. 1). The enclosures were built using bricks about 2.5 m high above ground and 0.5 m below the soil surface. The walls were coated with cement to prevent climbing by the animals and the top of the enclosure was covered with plastic nets to prevent access by predators.
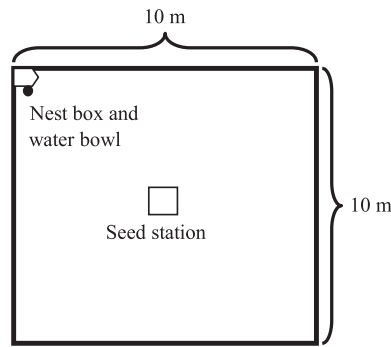
Fig. 1: Diagraph of one of the semi-natural enclosures previously established in the experimental area.

To determine whether or not pericarp removal influences scatter-hoarding behavior, we provided each of 16 Siberian chipmunks with ten pairs of tagged intact and shelled acorns (removed by observers) in the center of the arena to determine caching preferences. Each animal was released into one enclosure between 07:30 h to 08:00 h on the day of the experiment. All animals were fed prior to placement in enclosures, and acorns placed in the enclosure were the only food source available to the animal during the experimental trial. We checked the acorns at the end of each trial (17:00 h). Seed fates were classified into seven categories according to previous observations (Yi & Zhang 2008a) with minor modifications: (1) intact *in situ*, (2) eaten *in situ*; (3) eaten after dispersal, (4) intact after dispersal (on the ground surface); (5) cached after dispersal (in the soil), (6) total dispersed (eaten after dispersal, intact after dispersal, and cached after dispersal), and (7) total consumed (eaten *in situ* and eaten after removal). We recorded the number of intact and pericarp-removed acorns that were dispersed, consumed, and cached.

To determine the effects of pericarp removal on acorn germination, we compared germination rates for shelled and unshelled acorns. We randomly selected 100 intact acorns and 100 pericarp-removed acorns from a composite sample of acorns that were shelled by Siberian chipmunk. Twenty flowerpots (diameter = 20 cm, height = 15 cm) each prepared with forest soil were divided into two groups, and 10 acorns of each treatment (intact and pericarp-removed) were uniformly sown 1 cm deep in each of 10 pots. All the pots were kept in natural conditions and the germination rates were recorded after 15 d of cultivation.

To test whether or not pericarp removal prevents pilferage or facilitates cache recovery, we prepared

artificial caches of intact and shelled acorns (pericarp-removed by chipmunks and experimentally) and then recorded pilfering rates by individual Siberian chipmunks in semi-natural enclosures. Ten intact and ten pericarp-removed acorns were buried 1–2 cm in depth at random locations in each of seven of the semi-natural enclosures early morning on a single day during the study. Seven randomly selected chipmunks were then each released into one of seven enclosures immediately following acorn placement (approx. 08:00 h). This sample was limited by the availability of chipmunk-shelled acorns. The proportion of remaining acorns and the pilfering rates in each of the seven enclosures were assessed at 17:00 h after chipmunk removal. Similarly, we also provided 30 caches containing one intact and one pericarp-removed acorn (pericarp-removed by chipmunks and experimentally) to each of six *A. peninsulae*, to see if pericarp removal of acorns influenced interspecific pilfering.

To determine whether or not odor in the pericarp influences acorn selection and scatter hoarding, we provided ten pairs of intact and acetone-treated acorns to each of 16 chipmunks. We first removed the pericarps of the treated acorns and soaked their pericarps in acetone for 48 h prior to their reattachment. Acorn shells were carefully cut, treated, and re-attached following the procedures of Steele et al. (2001a). Controls were whole intact acorns. Similar to the procedure of the first experiment, acorns were released at the seed station in each enclosure. A single chipmunk was released into each enclosure for 1 d, after which we recorded the number of the two acorn types removed, consumed, and cached.

To test whether pericarp removal causes rapid leaching or decomposition of tannins in acorns, we randomly selected 50 intact and 50 pericarp-removed acorns by chipmunks from composite samples. We then buried each of these 100 acorns in individual, artificial caches in the field, simulating the microenvironments and depth (1–2 cm) of natural caches and exposing the acorns to rain for potential leaching of tannins. After 30 d, acorns were recovered and dried at 60–70°C for 48 h and sent to the Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences for tannin measurement. Tannin concentrations were calculated using the Folin-Denis method (AOAC 1990).

Seed perishability has been recognized as an especially important factor influencing hoarding decision of rodents (Fox 1982; Hadj-Chikh et al. 1996), and infestation by weevils, in particular, has been shown to influence caching decisions by scatter hoarders

(Steele et al. 1996). To test whether or not Siberian chipmunks rely on pericarp removal to discriminate between sound and infested acorns for scatter hoarding and maximize rewards from their caches, we provided each of 16 Siberian chipmunks with equal numbers (10 each) of intact acorns that were non-infested, infested but without obvious emergence holes, or infested with one or two emergence holes. We used water flotation and visual inspection to determine whether or not acorns were infested (Xiao et al. 2003). We again tested the response of individual chipmunks in separate 1-d trials in outdoor arenas. Following each trial with a chipmunk, we recorded the number of each type of acorn that was removed, consumed, or cached.

To ensure the ethical treatment of animals throughout the trials, our behavioral studies and housing procedures were approved by the Henan University of Science and Technology.

Statistics and Analysis

We used a general linear model (GLM), following arcsine transformation for all percentages, to evaluate differences in seed dispersal and pilfering rates between intact and pericarp-removed acorns, and to determine whether or not chipmunks treated infested and sound acorns differently. We also used GLM to evaluate the influence of acetone treatments on the number of acorns removed, consumed, and cached. We used One-way ANOVA (LSD, least significant difference) to compare effects of pericarp removal on germination rates, and tannin concentrations.

Results

Siberian chipmunks only cached pericarp-removed acorns. Siberian chipmunks removed the pericarp of intact acorns and cached them along with those from which the pericarps were experimentally removed by researchers. The original condition of these acorns (intact and pericarp-removed) did not influence the chipmunks' decision to disperse, cache or eat them (total dispersed: $F_{1,30} = 3.050$, p = 0.092; cached after dispersal: $F_{1,30} = 0.781$, p = 0.384; total consumed: $F_{1,30} = 3.867$, p = 0.059) (Fig. 2). Significantly more of the control acorns were found *in situ* (intact *in situ* and eaten *in situ*) than those dispersed (total dispersed) from the seed source ($F_{1,30} = 16.113$, p < 0.001). However, no difference was found between pericarp-removed acorns *in situ* and those removed ($F_{1,30} = 0.012$, p = 0.914) (Fig. 2), suggesting a preference for pericarp-removed acorns

for dispersal. Of the control acorns that had pericarps removed and were dispersed, more were cached (cached after dispersal/total dispersed) rather than eaten (eaten after dispersal/total dispersed) ($F_{1,30} = 7.302$, p = 0.012), although there was no difference in the number of acorns with experimentally removed pericarps that were cached and eaten ($F_{1,30} = 0.143$, p = 0.708), indicating that the chipmunks selectively cached acorns following pericarp removal.

Pericarp removal did not affect the germination rates (83.00 ± 2.90% vs. 85.00 ± 2.43%, $F_{1,18} = 0.175$, p = 0.681) or tannin concentrations (3.80 ± 0.16% vs. 3.94 ± 0.14%, $F_{1,8} = 0.401$, p = 0.544) of *Q. mongolica* acorns. Siberian chipmunks dispersed and cached control and acetone-treated acorns at equal rates: intact *in situ* ($F_{1,30} = 0.041$, p = 0.842), eaten *in situ* ($F_{1,30} = 0.048$, p = 0.827), cached after dispersal ($F_{1,30} = 0.320$, p = 0.576), total dispersed ($F_{1,30} = 0.060$, p = 0.808), and total consumed ($F_{1,30} = 0.396$, p = 0.534) (Fig. 3). Chipmunks consistently removed the pericarps of both control and acetone-treated acorns before caching. Furthermore, the rates of cache pilferage did not differ between the normal and pericarp-removed acorns ($F_{2,18} = 0.081$, p = 0.781) (Fig. 4). By providing a potential interspecific pilferer, *A. peninsulae,* with paired caches containing shelled or unshelled acorns, we found no difference in cache recovery rates ($F_{2, 15} = 0.696$, p = 0.514) (Fig. 4), suggesting that pericarp removal by Siberian chipmunks did not influence pilfering rates for this species.

Siberian chipmunks selected sound and infested acorns at equal rates in terms of the numbers of
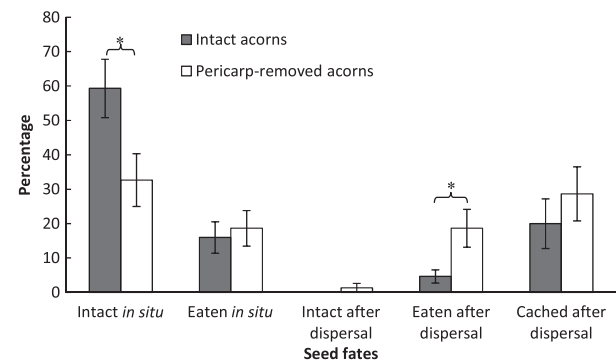
Fig. 2: Seed fates of intact and pericarp-removed acorns of *Quercus mongolica* manipulated by Siberian chipmunks. Data are expressed as mean ± SE. *, **, and *** on histograms indicate significant differences in seed fates between different types of acorns at p < 0.05, p < 0.01 and p < 0.001 levels, respectively. Note: all intact acorns that were cached first had pericarps removed by chipmunks.
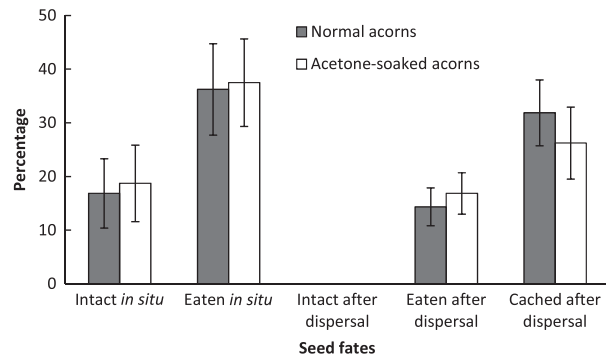
Fig. 3: Seed fates of normal and acetone-soaked acorns of *Quercus mongolica* following dispersal and consumption by Siberian chipmunks. Data are expressed as mean ± SE. All intact acorns that were cached first had pericarps removed by chipmunks.

Fig. 5: Seed fates of sound and infested acorns of *Quercus mongolica* manipulated by Siberian chipmunks. Data are expressed as mean - SE. *, **, and *** on histograms indicate significant differences in seed fates between different types of acorns at p < 0.05, p < 0.01 and p < 0.001 levels, respectively. Note: all intact acorns that were cached first had pericarps removed by chipmunks.

acorns remaining at the seed stations ($F_{2,46} = 0.386$, p = 0.682) (Fig. 5). There were significant differences between the number of sound and infested acorns that were cached or eaten (cached after dispersal: $F_{2,46} = 22.257$, p < 0.001; total consumed: $F_{2,46} = 10.882$, p < 0.001) (Fig. 5). Multiple comparisons indicated that more sound acorns were found to be cached than all types of infested acorns (all p < 0.001) and fewer sound acorns were eaten than each of the infested types (p = 0.001, p < 0.001). For sound acorns, we observed no difference between those found *in situ* (intact *in situ* and eaten *in situ*) and those dispersed (total dispersed) ($F_{1,30} = 0.154$, p = 0.698), however, more infested acorns were found *in situ* than removed (infested acorns without holes: $F_{1,30} = 394.071$, p < 0.001; with holes: $F_{1,30} = 393.202$, p < 0.001) (Fig. 5). Our results further indicated that Siberian chipmunks removed significantly more sound acorns for scatter hoarding than for eating ($F_{1,30} = 10.632$, p = 0.003) (Fig. 5), whereas, more
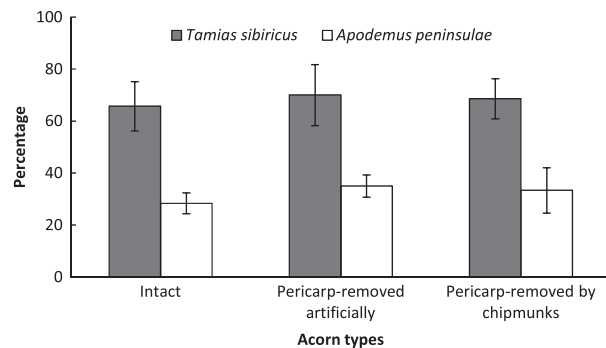
infested acorns were found to be eaten than scatter hoarded (infested acorns without holes: $F_{1,30} = 262.716$, p < 0.001; with holes: $F_{1,30} = 210.172$, p < 0.001), indicating that the animals preferentially scatter hoarded non-infested acorns.

Discussion

Seed perishability is recognized as a key factor influencing the caching strategies of many food-hoarding animals (Hadj-Chikh et al. 1996; Steele et al. 2001b; Xiao et al. 2009). However, our results clearly showed that pericarp removal failed to prevent or postpone acorn germination, indicating that pericarp removal does not serve the same role as embryo excision or radicle pruning in the long-term management of seed caches (Fox 1982; Steele et al. 2001b; Jansen et al. 2006; Xiao et al. 2009). Selection of pericarp-removed acorns may save time (reduce foraging costs) and reduce the risk of predation at a seed source. However, time-savings alone could not account for the chipmunk's preference for pericarp-removed acorns. Although more pericarp-removed acorns were removed from seed stations, which support both the perishability and time-savings hypotheses (Jacobs 1992; Steele et al. 1996), significantly more of the pericarp-removed acorns were cached rather than eaten, supporting the former hypothesis.

Scatterhoarding rodents (e.g., chipmunks and squirrels) are thought to rely on olfaction, spatial memory, and/or exploratory digging to recover their caches (Vander Wall 1991, 2000; Clarke & Kramer 1994; Winterrowd & Weigl 2006; Steele et al. 2011). Results of acetone treatments on acorn caching and

Fig. 4: Cache recovery and pilferage of intact and pericarp-removed acorns of *Quercus mongolica* by *Tamias sibiricus* and *Apodemus peninsulae*. Data are expressed as mean ± SE.
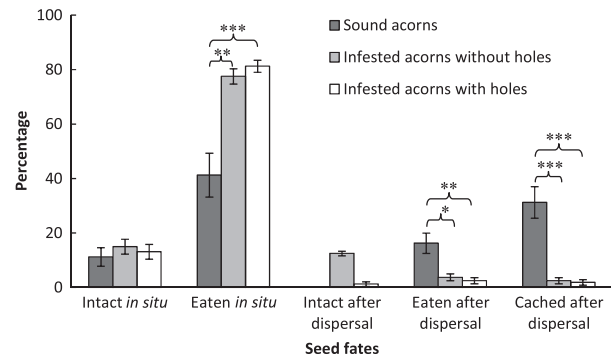
pericarp removal on rates of cache pilferage strongly suggest that olfactory cues in the pericarp or cotyledons do not aid significantly in pilferage or relocation of caches. Pericarp removal shows no significant effect on interspecific pilfering by *A. peninsulae*, indicating that chipmunks were not attempting to prevent pilferage by conspecifics and other species. Thus, pericarp removal seems to function in a different way from pulp removal of fleshy seeds by rodents (Guimarães et al. 2005; Jansen et al. 2010). Moreover, pericarp removal did not result in a reduction of tannin concentrations of *Q. mongolica* acorns, allowing us to reject the tannin decomposition hypothesis.

Some rodents and birds have evolved specific behaviors to assess seed quality (e.g., infested seeds) before caching through 'bill-clicking', 'bill-weighing', 'head flicking', and/or assessment by olfactory cues (Johnson et al. 1987; Steele et al. 1996; Preston & Jacobs 2009). In our study, significantly more sound than infested acorns were pericarp-removed and then scatter hoarded by chipmunks, strongly suggesting that Siberian chipmunks rely on pericarp removal to determine acorn quality and whether to scatter-hoard or eat individual acorns. Despite other studies that have shown that seed-eating mammals and birds have a high degree of accuracy in rejecting infested seeds (Vander Wall 1990; Steele et al. 1996; Dixson et al. 1997; Xiao et al. 2003; Wang & Gao 2006; Muñoz & Bonal 2008), results in our study strongly suggested that Siberian chipmunks were unable to distinguish between infested and sound acorns when intact; equal proportions of sound and infested intact acorns remained at seed stations. Eastern gray squirrels (*S. carolinensis*) and Edward's long-tailed rats (*Leopoldamys edwardsi*) may not always discriminate infested acorns (Weckerly et al. 1989; Cheng & Zhang 2011; but Steele et al. 1996). Our results, however, showed that Siberian chipmunks removed the pericarp of acorns before they dispersed and cached them (see Videos S1 and S2), suggesting that chipmunks can avoid the cost of caching infested acorns by removing the pericarps first. Thus, it appears pericarp removal was a prerequisite for determining acorn infestation. Nearly all acorns were pericarp-removed before they were dispersed from seed stations, further supporting our hypothesis.

Although it is possible that pericarp removal allows chipmunks to opportunistically supplement their protein by consuming insects as suggested for other scatter hoarders (Steele et al. 1996), our results fail to support this as a primary explanation for pericarp removal. Siberian chipmunks preferred pericarp-removed acorns over those that were intact, and never discarded sound, chipmunk-shelled acorns. Nevertheless, the chipmunks appeared to incidentally consume insects when feeding on infested acorns.

One may argue that pericarp removal might lower the mass of the acorn and therefore reduce the cost of transport. If this was true, chipmunks would disperse and then cache more pericarp-removed acorns than intact acorns. However, we found no significant difference in the proportions of the two types of acorns dispersed (total dispersed) or those cached after dispersal. Although in our study, pericarps were often removed prior to dispersal and caching, pericarp mass typically accounts for <11% of total acorn mass. Thus, we do not believe transport cost would be a major factor influencing pericarp removal. We therefore conclude that the most plausible explanation of pericarp removal by Siberian chipmunks is to ensure successful storage of sound acorns.

We predict that pericarp removal and caching of sound acorns would benefit at least early acorn germination and possibly seedling establishment of *Q. mongolica* because sound acorns exhibit far higher germination rates than those of infested acorns (Yi & Zhang 2008b). Furthermore, Siberian chipmunks universally remove pericarps of *Q. mongolica* acorns and selectively consume infested acorns, posing strong predation pressure on weevils and other insect acorn predators. Thus, pericarp removal may regulate these insect populations and at the same time enhance dispersal of *Q. mongolica*. Future studies will be directed at quantifying the potential impact of pericarp removal on acorn insect predator populations and long-term patterns of seed survival and establishment in this oak species.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1. Siberian chipmunks shelling tagged acorns.

Video S2. Siberian chipmunks shelling untagged acorns.

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