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ORIGINAL PAPER

The combined effects of seed perishability and seed size on hoarding decisions by Pére David's rock squirrels

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Abstract The food perishability hypothesis reasons that the perishability of nondormant acorns through rapid germination is the primary determinant of hoarding decisions (e.g., embryo removal in nondormant acorns in particular) by scatter-hoarding squirrels. However, we do not know whether seed size and its interactions with seed germination schedule affect squirrel's hoarding decisions. By presenting pairs of acorns with contrasting germination/dormancy conditions and seed size, we investigated the relative importance of each target trait in determining the hoarding decisions of free-ranging Pére David's rock squirrel (*Sciurotamias davidianus*) in Central China. Consistent with the food perishability hypothesis, the squirrels were highly sensitive to subtle differences of acorn germination status either within nondormant acorns or between nondormant and dormant acorns. Though there were no significant differences in seed hoarding and dispersal distance, the embryo-removal probability of nondormant acorns (especially those germinated) was much higher than that of dormant acorns prior to hoarding. Our results also support the seed size hypothesis. Large acorns were often hoarded more and moved farther than small acorns, and large nondormant acorns also had a higher probability of having their embryos removed. Moreover, the interactions between seed size and seed germination schedule had a large effect on whether a given acorn was hoarded or hoarded with its embryo removed. Our study indicates that the combined effects from seed germination schedule and seed size have the potential to determine hoarding decisions of scatter-hoarding squirrels.

Keywords Germination schedule · Oaks *Quercus* · Pére David's rock squirrel *Sciurotamias davidianus* · Scatter-hoarding · Seed size

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Introduction

Scatter-hoarding of seeds or other food items is widely accepted as an adaptive behavior for many rodents and birds across a wide range of habitats (Vander Wall 1990). It is well known that the characteristics of food items can largely affect foraging decisions of hoarding animals (Smith and Reichman 1984; Preston and Jacobs 2009). Growing evidence suggests that the perishability of a given food item, i.e., potential loss of energy and nutrients during storage caused by decomposers, insect infestation, or seed germination, is the primary determinant of hoarding decisions by scatter-hoarding animals (the food perishability hypothesis, Reichman 1988; Gendron and Reichman 1995, Hadj-Chikh et al. 1996; Steele et al. 1996, 2006; Xiao et al. 2009, 2010).

Within a given community, some seed species produce *nondormant* seeds that can germinate with visible sign (i.e., the radicle protruding from seed coat or pericarp) at or shortly after maturity, while others produce *dormant* seeds that undergo an extended period with no visible sign of sprouting and then germinate the following spring or even much later (Vázquez-Yanes and Orozco-Segovia 1993; Farnsworth 2000). The germination or dormancy of seeds has been frequently reported to have fundamental impacts on foraging decisions of many scatter-hoarding animals. A number of squirrel species, for example from the genus

Sciurus in North America, Eastern gray squirrel (*Sciurus carolinensis*), red-bellied squirrel (*Sciurus aureogaster*), and fox squirrel (*Sciurus niger*) (Fox 1982; Steele et al. 2001a), and in China, Pallas's squirrel (*Callosciurus erythraeus*), Pére David's rock squirrel (*Sciurotamias davidianus*) and Asian red-cheeked squirrel (*Dremomys rufigenis*) (Xiao et al. 2009, 2010; Xiao and Zhang 2012), have been found to display the same specific behavior of embryo removal from nondormant acorns of white oaks (section *Quercus*) in both Asia and North America, compared to dormant acorns from red oaks (section *Lobatae*) in North America and Qinggang oaks (section *Cyclobalanopsis*) in Asia. In addition, other rodent species have been found to display similar behavior to prevent or delay seed germination during the hoarding process (eastern chipmunk (*Tamias striatus*) to *Fagus granifolia* seeds in North America (Elliott 1978), red acouchi (*Myoprocta exilis*) to *Carapa procera* seeds in South America (Jansen et al. 2006), and *Maxomys surifer* and other rodent species to *Pittosporopsis kerrii* seeds in southwest China (Cao et al. 2011). Chang et al. (2009) also showed that Edward's long-tailed rats (*Leopoldamys edwardsi*) and South China field mice (*Apodemus draco*) hoarded more dormant acorns over nondormant acorns or hoarded more non-germinated acorns than germinated acorns within nondormant acorns. These studies underscore the general conclusion that many distinct species have evolved behavioral strategies (e.g., embryo removal) in order to use nondormant seeds for long-term storage.

The food perishability hypothesis has been strongly supported as an adaptive mechanism to explain why scatter-hoarding squirrels evolved the embryo removal behavior to nondormant acorns compared to dormant acorns (Fox 1982; Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001a, b, 2006; Xiao et al. 2009, 2010, 2013; Xiao and Zhang 2012). The food perishability hypothesis makes two key predictions: (a) dormant acorns should be hoarded more and dispersed farther than nondormant acorns (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001a, 2006) and (b) the embryo-removal probability of nondormant acorns should be higher than that of dormant acorns (Fox 1982). In this study, we expect that these predictions would be supported not only when using dormant Qinggang oak acorns and nondormant white oak acorns, but also when using germinated and non-germinated acorns within nondormant white oak acorns.

Besides seed germination schedule, there are other characteristics (tannin level and seed size) in acorns and other seeds that can also affect foraging decisions (Smallwood and Peters 1986; Xiao et al. 2008, 2009; Chang et al. 2009). Xiao et al. (2009) showed that tannin level had no strong effects on embryo removal by squirrels though it had a large effect on animal feeding and hoarding. However, we do not know whether seed size affects embryo removal of nondormant white oak acorns by squirrels, and whether its interactions with seed germination schedule can also affect squirrel's hoarding decisions. The large seed size hypothesis (= the handling time hypothesis) reasons that larger acorns accommodate more nutrients than smaller ones but need more time to be consumed, and thus they are most preferred to be hoarded and dispersed farther (Hadj-Chikh et al. 1996; Jansen et al. 2004; Xiao et al. 2005; Chang et al. 2009). All else being equal, we thus expect that if scatter-hoarding squirrels use nondormant white oak acorns as long-term storage for periods of food shortage, the probability of embryo removal may be higher for larger acorns than smaller acorns.

By presenting pairs of acorns with contrasting germination/dormancy conditions and seed size in a deciduous broadleaf forest in Central China, we investigated the relative importance of each target trait in determining hoarding decisions of free-ranging Pére David's rock squirrels. Pére David's rock squirrel is endemic in China and has been less studied until recently. This squirrel is a typical scatter-hoarder of acorns and other nuts (Lu and Zhang 2005; Xiao et al. 2010, 2013; Huang et al. 2011). Recently, we found that this squirrel can also remove the embryo of acorns and chestnuts (Xiao et al. 2010, 2013). Based on the two hypotheses above, we conducted three sets of experiments: (1) *Experiment I* was to test the effects of seed germination status (germinated vs. non-germinated) and seed size on squirrels' hoarding decisions with only nondormant white oak acorns; (2) *Experiment II* was to test the effects of seed size on squirrels' hoarding decisions with only nondormant white oak acorns; and (3) *Experiment III* was to test the effects of seed size and seed germination schedule (dormant vs. nondormant) on squirrels' hoarding decisions with both dormant Qinggang oak acorns and nondormant white oak acorns. In particular, we aimed to test how seed size and seed germination schedule act together to determine squirrels' hoarding decisions.

Materials and methods

Study site

We carried out field experiments during autumn (late September to November) of 2008 and 2009 in the Foping National Nature Reserve (1,100–1,300 m; 35°0′N, 105°30′E) in Shaanxi Province, Central China. The reserve (ca. 293 km^2) was established in 1978 to conserve the endangered giant panda and its habitat. The total annual rainfall averages 920 mm with frequent rainfall from May to October, and the average annual temperature is about 13 °C with an extreme low temperature of −3 °C in January and an extreme high temperature of 28 °C in July. The main natural vegetation types in the reserve include deciduous broadleaf forests (below

2,000 m), birch forests (2,000–2,500 m) and conifer forests (above 2,500 m) (Liu and Zhang 2003). In deciduous broadleaf forests, several oak species (e.g., white oaks, *Quercus aliena* var. *acutesevata*, *Quercus serrata* var. *breviptiolata*, *Quercus variabilis*, *Quercus serrata*, *Quercus spinosa*, and *Quercus engleriana*; and Qinggang oaks, *Cyclobalanopsis multinervis*, *Cyclobalanopsis breviradiata*, and *Cyclobalanopsis glauca*) and other nut-bearing plants (e.g., *Castanea mollissima*, *Corylus* spp. and *Juglans* spp.) are common (Liu and Zhang 2003). These nut-bearing plants provide rich food sources (seeds) for local animals such as Pére David's rock squirrel, Swinhoe's striped squirrel (*Tamiops swinhoei*), white-bellied rats (*Niviventer confucianus*), South China field mouse (*Apodemus draco*), and greater long-tailed hamster (*Tscheskia triton*) (Liu and Zhang 2003).

Experimental design

In this study, we used four common oak species with two nondormant white oaks (*Q. aliena* var. *acutesevata* and *Q. serrata* var. *breviptiolata*) and two dormant Qinggang oaks (*C. multinervis* and *C. breviradiata*). The four oak species also had two types of seed size: *Q. aliena* var. *acutesevata* and *C. breviradiata* produce larger acorns than either *Q. serrata* var. *breviptiolata* or *C. multinervis* (one-way ANOVA with LSD: $F_{3,116}=550.1$, $P<0.001$; Table 1). In addition, all four oak species produce acorns with high-tannin levels (over 8 %) (Table 1).

After maturity, we collected acorns from several fruiting plants for each species. All acorns from *C. breviradiata* and *C. multinervis* were dormant and did not germinate for each paired trial, but *Q. aliena* var. *acutesevata* and *Q. serrata* var. *breviptiolata* acorns either germinated with the radicle protruding from the pericarp or did not germinate for each paired trial. Here, germinated acorns had radicles protruding from the pericarp for white oak acorns only, and non-germinated acorns showed no visible signs of germination for white oak acorns or remained dormant for Qinggang oak acorns during the experimental period. From late September to mid-November in 2008 and 2009, we conducted three sets of experiments to investigate how Pére David's rock squirrels utilized acorns with contrasting germination conditions and/or seed size (Table 2):

> Experiment I was to test the effects of seed germination status and seed size on squirrels' hoarding decisions. Only nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) and *Q. serrata* var. *breviptiolata* (small size) were used and these acorns also included two contrasting germination status (non-germinated vs. germinated). We had eight acorn-pair trials including 400 acorns.
>
> Experiment II was to test the effects of seed size on squirrels' hoarding decisions. Only nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) and *Q. serrata* var. *breviptiolata* (small size) were used, but only non-germinated acorns were included for *Q. aliena* var. *acutesevata*, and both non-germinated and germinated acorns were included for *Q. serrata* var. *breviptiolata*. We had six acorn-pair trials including 300 acorns.
>
> Experiment III was to test the effects of seed germination schedule (dormant vs. nondormant) and seed size on squirrels' hoarding decisions with both dormant acorns from *Cyclobalanopsis multinervis* (small size) and *C. breviradiata* (large size) and nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) or *Q. serrata* var. *breviptiolata* (small size). Here, nondormant acorns also included two contrasting germination status (non-germinated vs. germinated). We had 14 acorn-pair trials including 700 acorns with contrasting germination schedules and seed size.

For each paired trial, we selected 25 sound acorns for each germination status or seed size category and labeled them individually with a numbered plastic tag attached by a thin stainless steel wire 10 cm long (plastic tags were used rather than tin tags) (Xiao et al. 2006b). Since squirrels were diurnal, we began at 0830 to 0930 hours and monitored until 1530 hours. For each trial, we placed the 50 tagged acorns (25 acorns for each acorn type) randomly distributed in a circle (diameter, ca. 0.5 m) on the ground. Acorn fate was checked at each trial (the search radius: ca. 30 m). Acorns at each trial were categorized as remaining, eaten, and removed, while those removed from the source were categorized as hoarded, eaten (tags and seed fragments found), or missing (not retrieved). Hoarded acorns were also excavated to identify whether their embryos were removed by animals. Distances to the source were also measured for the hoarded and eaten acorns. To identify which animals were most responsible for the hoarding and embryo removal of the tagged acorns, we used a digital Video Camera (Sony DCR-SR85E) for up to ten trials (total 20 h). From the video camera data, we found that one to three squirrels harvested nearly all of the tagged acorns for each trial (see also Xiao *et al*. 2010). The trials were conducted in six different isolated stands (area, 5–15 ha., separated 1–5 km from each other), and each trial was also conducted at a different location in different stands to avoid any biases that would result from the squirrels' experience. Successive trials at the same stand were performed 3–5 days after previous trials depending on to weather conditions. On transect surveys (30 min) we found at least 5–8 individual squirrels at each stand.

Data analysis

We used three behavioral parameters to assess squirrels' hoarding decisions: (1) the proportion of total acorns that were hoarded (including those with embryo removal), (2) the

Table 1 The characteristics of acorns from oaks (*Quercus* sensu lato, including white oaks and Qinggang oaks) in Qinling Mountain, Central China

Oak group/species	Germination schedule	Fat (%)[a]	Tannin (%)[a]	Seed size (mean ± SE g)[b]
White oaks (section *Quercus*)				
Quercus serrata var. *breviptiolata*	Nondormant	1.4	7.9	Small (1.01±0.07)a
Quercus aliena var. *acutesevata*	Nondormant	1.5	9.7	Large (1.83±0.05)b
Qinggang oaks (section *Cyclobalanopsis*)				
Cyclobalanopsis multinervis	Dormant	3.4	8.0	Small (1.06±0.02)a
Cyclobanopsis breviradiata	Dormant	1.40	9.1	Large (1.78±0.03)b

[a] Fat and tannin content (%) were related to dry kernels

[b] Different letters (a, b) indicate significant differences between any two of the four seed species (one-way ANOVA with LSD: $F_{3,116}$=550.1, P<0.001)

proportion of the hoarded acorns that had the embryo removed, and (3) dispersal distance (m) to the source for all hoarded acorns. The behavioral parameters 1–2 were binary data, and thus were analyzed using generalized linear mixed models with binomial errors. Dispersal distance data were log-transformed to meet the normality and were analyzed using generalized linear mixed models with Gaussian errors. In *Experiment I*, seed germination status (germinated vs. non-germinated) and seed size (large vs. small) were treated as fixed factors with seed germination status nested within seed size and trial as random factors; in *Experiment II*, seed size (large vs. small) was treated as a fixed factor with seed germination status and trial as random factors; and in *Experiment III*, seed germination schedule (dormant vs. nondormant) and seed size (large vs. small) were treated as fixed factors with seed germination status and trial as random factors. In this study, we used the Akaike information criterion for model selection to remove the interactions between seed germination schedule and seed size for each behavioral parameter in *Experiment I* and *Experiment III* (Crawley 2007). In addition, we also estimate effect size for each behavioral parameter and each experiment as suggested by Nakagawa and Schielzeth (2013): marginal R^2 (R^2(m)) and conditional R^2 (R^2(c)). Generalized linear mixed models were carried out in R (version 2.13.1, R Core Team 2012) program with package lme4 (Bates et al. 2012).

Results

Effects of seed germination status and seed size with only nondormant acorns

In *Experiment I*, large acorns were hoarded more than small acorns, but seed germination status had no significant effects on seed hoarding (Fig. 1a; Table 3). However, the proportion of the hoarded seeds that had the embryo removed was much higher for the germinated acorns than that for the non-germinated acorns, and the interaction between seed germination status and seed size also significantly affected the embryo-removal probability (Fig. 1b; Table 3). In addition, dispersal distance of the hoarded acorns was much longer for non-germinated acorns than that for germinated acorns (Fig. 1c; Table 3).

Table 2 Experimental design for how seed perishability (seed germination/dormancy condition) and seed size affect squirrels' hoarding decisions (including embryo removal). Seed samples were shown for each acorn species

Seed size	Seed perishability	
Experiment I: Effects of seed size and seed germination status with only nondormant acorns		
	Non-germinated	Germinated
Small (200 seeds)	*Quercus serrata* var. *breviptiolata* (100 seeds)	*Quercus serrata* var. *breviptiolata* (100 seeds)
Large (200 seeds)	*Quercus aliena* var. *acutesevata* (100 seeds)	*Quercus aliena* var. *acutesevata* (100 seeds)
Experiment II: Effects of seed size with only nondormant acorns		
	Nondormant (non-germinated + germinated)	
Small (150 seeds)	*Qurecus serrata* var *breviptiolata* (75+75=150 seeds)	
Large (150 seeds)	*Quercus aliena* var. *acutesevata* (150 seeds)	
Experiment III: Effects of seed size and seed germination schedule with dormant and nondormant acorns (nondormant acorns included those germinated and non-germinated)		
	Dormant	Nondormant (non-germinated + germinated)
Small (250 seeds)	*Cyclobalanopsis multinervis* (125 seeds)	*Qurecus serrata* var. *breviptiolata* (50+75=125 seeds)
Large (450 seeds)	*Cyclobanopsis breviradiata* (225 seeds)	*Quercus aliena* var. *acutesevata* (150+75=225 seeds)

Effects of seed size with only nondormant acorns

In *Experiment II*, large acorns had pronounced effects on squirrels' hoarding decisions compared to small acorns: large acorns were hoarded more and dispersed farther, and also had a higher embryo-removal probability (Fig. 2; Table 4).

Effects of seed germination schedule and seed size with dormant and nondormant acorns

In *Experiment III*, large acorns were hoarded more than small acorns, and this difference was more pronounced for dormant acorns relative to nondormant acorns (Fig. 3a; Table 5). The embryo-removal probability was significantly higher for nondormant acorns than for dormant acorn, but it was marginally higher for large acorns than for small acorns (Fig. 3b; Table 5). In addition, the interaction between seed size and seed germination schedule also had a significant effect on the embryo-removal probability (Table 5). However, large acorns were dispersed shorter than small acorns, but seed germination schedule had no significant effects on dispersal distance (Fig. 3c; Table 5).

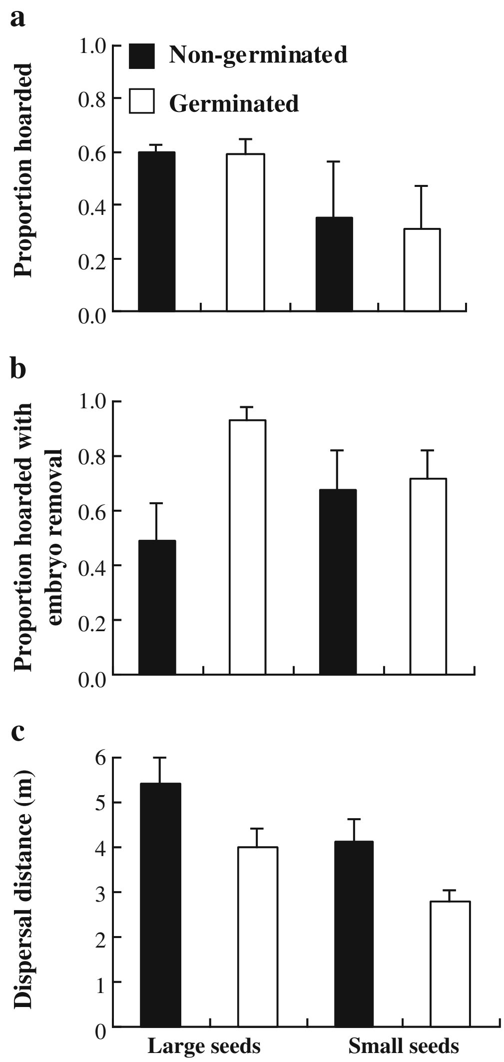

Fig. 1 Effects of seed germination status (non-germinated vs. germinated) and seed size (large vs. small) on hoarding decisions by Pére David's rock squirrels with only nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) and *Quercus serrata* var. *breviptiolata* (small size). Behavioral parameters include **a** proportion of acorns hoarded, **b** proportion of the hoarded acorns that had their embryo removed, and **c** dispersal distance (m) from the source for all hoarded acorns. All bars are mean±1 SE

Table 3 Statistical results from generalized linear mixed models with seed germination status and seed size as fixed factors and seed germination status nested seed size and bout as random factors for each behavioral parameter (see details in text; *Experiment I*). Effect size for each behavioral parameter includes marginal R^2 (R^2 (m)) and conditional R^2 (R^2 (c)). Fixed factors in bold indicate significant differences ($P<0.05$)

Fixed factor	Estimate ± SE	z	*P*
Hoarded: R^2(m)=0.110 and R^2(c)=0.210			
Intercept	0.77±0.38	2.04	0.041
Seed size	**−1.34±0.23**	**−5.86**	**<0.001**
Germination	−0.18±0.22	−0.79	0.428
Hoarded with embryo removal: R^2(m)=0.261 and R^2(c)=0.444			
Intercept	2.88±0.73	3.93	<0.001
Seed size	−0.92±0.65	−1.41	0.160
Germination	**−3.03±0.60**	**−5.05**	**<0.001**
Seed size: Germination	**2.66±0.83**	**3.22**	**0.001**
	Estimate±SE	t	*P*
Dispersal distance: R^2(m)=0.040 and R^2(c)=0.261			
Intercept	0.90±0.27	3.35	<0.05
Seed size	0.27±0.15	1.72	>0.05
Germination	**0.34±0.13**	**2.55**	**<0.05**

Discussion

Our results with Pére David's rock squirrels provide sound evidence for the embryo removal prediction from the food perishability hypothesis (see also Fox 1982; Steele et al. 2001a; Xiao and Zhang 2012): compared to dormant Qinggang oak acorns (0–21 %), nondormant white oak acorns had a much higher embryo-removal probability (60–100 %). This prediction is also supported when only nondormant white oak acorns were presented: germinated acorns had a higher embryo-removal probability (58–100 %) than non-germinated acorns (14–100 %) (Fig. 1; see also Xiao and Zhang 2012). However, we found that there were no significant differences in seed hoarding and dispersal distance between dormant Qinggang oak acorns and nondormant white oak acorns. This is not consistent with the studies from North America that dormant red oak acorns are hoarded more and dispersed farther than

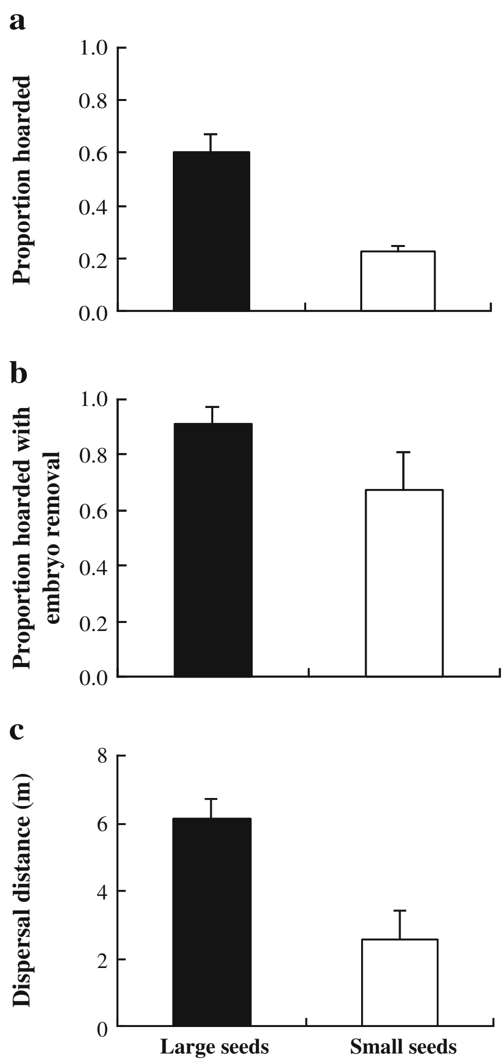

Fig. 2 Effects of seed size (large vs. small) on hoarding decisions by Pére David's rock squirrels with nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) and *Quercus serrata* var. *breviptiolata* (small size). Behavioral parameters include **a** proportion of acorns hoarded, **b** proportion of the hoarded acorns that had their embryo removed, and **c** dispersal distance (m) from the source for all hoarded acorns. All bars are mean±1 SE

nondormant white oak acorns (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001a, 2006), though we did find that non-germinated acorns were moved farther than germinated acorns when they were from nondormant white oak acorns. Therefore, our results indicate that seed germination schedule either within nondormant acorns or between nondormant and dormant acorns can have a pronounced effect on whether a given acorn is hoarded with the embryo removed or not, but its effects on seed hoarding and dispersal distance may be intertwined with other seed traits (e.g., tannin level, Xiao et al. 2009; seed size, see below) or other environmental factors (e.g., seed abundance, Xiao et al. 2013).

The important finding from our study is that seed size alone and its interactions with seed germination schedule

Table 4 Statistical results from generalized linear mixed models with seed size as a fixed factor and seed germination status and bout as random factors for each behavioral parameter (see details in text; *Experiment II*). Effect size for each behavioral parameter includes marginal R^2 (R^2(m)) and conditional R^2 (R^2(c)). Fixed factors in bold indicate significant differences (P<0.05)

Fixed factor	Estimate ± SD	z	*P*
Hoarded: R^2(m)=0.203 and R^2(c)=0.203			
Intercept	0.62±0.18	3.45	<0.001
Seed size	**−1.83±0.27**	**−6.89**	**<0.001**
Hoarded with embryo removal: R^2(m)=0.230 and R^2(c)=0.489			
Intercept	3.73±0.87	4.311	<0.001
Seed size	**−2.90±0.73**	**−4.00**	**<0.001**
	Estimate±SE	t	*P*
Dispersal distance: R^2 (m)=0.322 and R^2 (c)=0.574			
Intercept	1.88±0.57	3.30	<0.05
Seed size	**−2.04±0.29**	**−7.00**	**<0.001**

had significant effects on squirrels' hoarding decisions (e.g., hoarding probability and embryo-removal probability) either within nondormant white oak acorns (*Experiment I* and *II*) or between dormant Qinggang oak acorns and nondormant white oak acorns (*Experiment III*). Our results were most consistent with the seed size hypothesis. First, seed size had a pronounced effect on seed hoarding: large acorns from either dormant Qinggang oak acorns or nondormant white oak acorns often had a higher probability to be hoarded (*Experiments I–III*). In addition, the prediction that large acorns have a longer dispersal distance is only confirmed when seed size was the key factor (*Experiments II*), but not when both seed germination schedule and seed size were involved at the same time (*Experiments II* and *III*). This inconsistence about dispersal distance may be partly due to the combined effects from both seed germination schedule and seed size. Second, the embryo-removal probability of large white oak acorns (here *Q. aliena* var. *acutesevata*) was also much higher than that of small white oak acorns (*Q. serrata* var. *breviptiolata*) (*Experiments I–III*). This indicates that in addition to seed germination schedule, seed size also has a strong effect on the hoarding decisions of scatter-hoarding squirrels. In North America, however, one similar study reported that hoarding decisions of Eastern gray squirrels were less affected by seed size (handling time), but no data were provided to determine whether seed size had any effect on the squirrels' embryo-removal behavior (Hadj-Chikh et al. 1996).

For hoarding animals, it is important to balance immediate consumption of seeds against hoarding for later use due to seasonal changes in weather and food availability (Smith and Reichman 1984; Vander Wall 1990). Thus, the evolution of any foraging behaviors (feeding or hoarding) in animals may be dependent on what to eat and hoard over

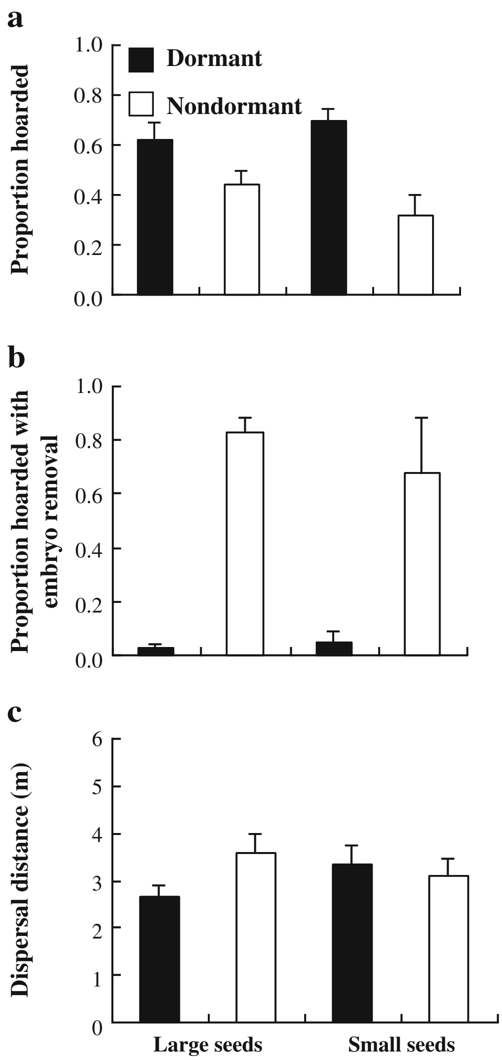

Fig. 3 Effects of seed germination schedule (dormant vs. nondormant) and seed size (large vs. small) on hoarding decisions by Pére David's rock squirrels with both dormant acorns from *Cyclobalanopsis multinervis* (small size) and *Cyclobalanopsis breviradiata* (large size) and nondormant acorns from *Quercus aliena* var. *acutesevata* (large size) or *Quercus serrata* var. *breviptiolata* (small size). Here, nondormant acorns included both non-germinated and germinated acorns. Behavioral parameters include **a** proportion of acorns hoarded, **b** proportion of the hoarded acorns that had their embryo removed, and **c** dispersal distance (m) from the source for all hoarded acorns. All bars are mean±1 SE

time and space. In general, foraging decisions made by hoarding animals are highly related to the whole food items (e.g., seeds), not just a separate seed trait. This means that though any single seed trait can have strong effects on related foraging behaviors, hoarding animals may make foraging decisions depending on the combined effects from all key seed traits (i.e., the seed itself). Based on our study and many other studies (Forget et al. 1998; Vander Wall 2003; Jansen et al. 2004; Xiao et al. 2005, 2006a), smaller seeds (lower food value) have a higher probability of being consumed first and larger seeds (with higher food value)

Table 5 Statistical results from generalized linear mixed models with seed germination schedule and seed size as fixed factors and seed germination status and bout as random factors for each behavioral parameter (see details in text; *Experiment III*). Effect size for each behavioral parameter includes marginal R^2 (R^2 (m)) and conditional R^2 (R^2 (c)). Fixed factors in bold indicate significant differences ($P<0.05$)

Fixed factor	Estimate ± SE	z	*P*
Hoarded: R^2(m)=0.110 and R^2 =(c)=0.181			
Intercept	0.22±0.27	0.82	0.414
Seed size	**0.61±0.18**	**3.34**	**<0.001**
Germination schedule	−0.15±0.15	−1.00	0.309
Seed size: germination schedule	**−1.78±0.25**	**−7.10**	**<0.001**
Hoarded with embryo removal: R^2(m)=0.575 and R^2(c)=0.680			
Intercept	−4.00±0.83	−4.81	<0.001
Seed size	1.15±0.61	1.88	0.061
Germination schedule	**5.92±0.58**	**10.30**	**<0.001**
Seed size: germination schedule	**−3.49±0.69**	**−5.07**	**<0.001**
	Estimate ± SE	t	*P*
Dispersal distance: R^2(m)=0.013 and R^2(c)=0.088			
Intercept	0.79±0.16	4.93	<0.05
Seed size	**0.28±0.11**	**2.60**	**<0.05**
Germination schedule	0.17±0.10	1.75	>0.05

have a higher probability of being removed and then hoarded and are dispersed farther. This seed hoarding strategy is consistent with the optimal foraging theory (Stephens and Krebs 1986). As shown before, rapid germination of nondormant white oak acorns can lead to nutrient and energy loss during hoarding. Studies from both China and North America strongly support the idea that the evolution of embryo removal behavior in scatter-hoarding squirrels is an effective strategy to deal with the evolution of nondormant acorns in white oaks (Fox 1982; Smallwood et al. 2001; Steele et al. 2001a, 2006; Xiao et al. 2009, 2010; Xiao and Zhang 2012). Combined squirrel's behaviors with acorn traits, our study indicates that the evolution of adaptive foraging behaviors by scatter-hoarding animals may be closely associated with the evolution of some key characteristics in seeds.

In conclusion, our study has demonstrated that in addition to seed germination schedule as the primary trait, seed size can also have a large effect on hoarding decisions (including embryo removal in nondormant acorns) by scatter-hoarding squirrels. Studies from both China and North America strongly support the idea that the evolution of embryo removal behavior in scatter-hoarding squirrels is a counter-adaptation to use nondormant white oak acorns for a long-term food supply. However, the evolution of nondormancy in white oaks presents a paradox because the nondormant phenotype seems a maladaptive trait for the dispersal of these oak species by squirrels. It is possible that the nondormant phenotypes may have a net advantage by escaping from post-dispersal predation through rapid germination for those dispersed acorns that retain intact embryos (Fox 1982). Xiao et al. (2010) suggested that white oak acorns may change the frequency of both dormant and nondormant phenotypes to increase escape from squirrel-induced mortality through frequency-dependent selection. Though each target acorn trait has strong impacts on hoarding decisions of scatter-hoarding squirrels, our study suggests that germination schedule and seed size can act together to determine whether a given acorn is hoarded or hoarded with its embryo removed.

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