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# Behavioral adaptation of Pallas's squirrels to germination schedule and tannins in acorns

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Using acorns from *Castanea henryi* (CH) and *Quercus variabilis* (QV) with contrasting germination schedule (related to food perishability) and tannin levels, we conducted field experiments in a subtropical forest in Southwest China to investigate how free-ranging Pallas's squirrels (*Callosciurus erythraeus*) utilize acorns as long-term storage based on the food perishability and high-tannin hypotheses. Though QV acorns germinated much earlier than CH ones, we found that Pallas's squirrels hoarded more high-tannin QV acorns over low-tannin CH ones, supporting the high-tannin hypothesis (but not the food perishability hypothesis). However, several other predictions derived from the food perishability hypothesis received sound support: nondormant QV acorns had their embryos removed with a higher probability (68.5%) than dormant CH ones (8.8%) and embryo-removed acorns had a much lower germination success but had a higher probability surviving as long-term storage. During the caching-recovery process, hoarding animals actively detected acorn state (dormant or not) and removed acorn embryos with an increasing probability in subsequent hoarding events. In addition, embryo-removed acorns could serve as long-term storage because they had a very low probability being infested by fungi as intact acorns did during the time of storage. We conclude that tree squirrels can differentially respond to acorn germination and remove the embryos of nondormant acorns more frequently as long-term storage, but tannin level is more important in determining whether a given acorn is hoarded or not. Combined with the studies from North America, our results suggest convergent evolution of acorn hoarding behavior in tree squirrels across different continents. *Key words:* behavioral decisions, germination schedule, long-term food supply, scatter hoarding, tannins, tree squirrels. *[Behav Ecol 20:1050–1055 (2009)]*

Many hoarding animals rely on plant seeds as food reserves for their survival and reproductive success (Smith and Reichman 1984; Vander Wall 1990). However, it is poorly understood how seed-hoarding animals, to adapt to considerable variation in seed availability and severe weather across seasons, manage their caches as long-term food supply based on the quantity and quality of seeds. Evidence suggests that hoarding animals are highly sensitive to food perishability because food value would decline during the time of storage due to the effects from decomposers (e.g., Reichman 1988; Gendron and Reichman 1995), insect infestation (e.g., Steele et al. 1996), and/or seed germination (e.g., Fox 1982; Hadj-Chikh et al. 1996; Steele, Turner, et al. 2001; Jansen et al. 2006).

For seed-hoarding animals, seed germination is one major cause of food perishability because energy reserves in seed cotyledons or endosperms are transported into a relatively indigestible taproot (Fox 1982; Hadj-Chikh et al. 1996; Steele, Turner, et al. 2001; Jansen et al. 2006; Steele et al. 2006). However, some hoarding animals are found to have evolved special behavioral strategies to deal with seed germination during hoarding process. One notable case is that in North America, several tree squirrel species from genus *Sciurus* are found to frequently remove the embryos of nondormant white oak acorns (subgenus *Quercus*), which germinate soon after falling on the ground or even on the tree after maturity compared with dormant acorns from red oak group (subgenus *Erythrobalanus*) (Fox 1982; Steele, Turner, et al. 2001; Steele et al. 2007). Several other rodent species are also found to display similar behavior to prevent or delay seed germination, for example, eastern chipmunks (*Tamias striatus*) to germinating *Fagus granifolia* seeds (Elliott 1978) and red acouchy (*Myoprocta exilis*) to germinating *Carapa procera* seeds (Jansen et al. 2006). However, acorn embryo removal by tree squirrels has never been reported outside North America though such behavior is believed as a counteradaptation to nondormant phenotype in white oaks, which co-occur with tree squirrels in many forests across the Northern Hemisphere.

Secondary compounds (e.g., tannins) in seeds also have important impacts on how hoarding animals use seeds as either short- or long-term food supply. As important food source for wildlife, acorns from many red oak species have a high level of tannins (6–10%), whereas those from many white oaks often have lower tannin content (0.5–2.5%) (Smallwood and Peters 1986; Smallwood et al. 2001), but some white oaks such as *Quercus variabilis*, *Quercus serrata*, and *Quercus mongolica* var. *grosseserrata* are found to produce high-tannin acorns (more than 8%) (Shimada 2001; Xiao et al. 2003; Shimada and Saitoh 2006). Tannins could cause severe detrimental effects such as interference in digestion, reduction in food palatability, kidney or liver failure, body weight loss, endogenous nitrogen loss, or even death on herbivores, including seed-hoarding animals (Shimada and Saitoh 2006 and references therein). To date, it is still argued what role acorn tannins play in hoarding decisions of related animals compared with other covarying acorn traits (e.g., germination schedule, acorn size, and fat content) between red oaks and white oaks (e.g., Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele, Smallwood et al. 2001; see also Xiao et al. 2008). Generally, acorn tannins

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are thought as chemical defense to deter feeding by insect and vertebrate seed predators (e.g., Smallwood and Peters 1986; Steele et al. 1993; Smallwood et al. 2001; Xiao et al. 2007, 2008), but high tannins in acorns may not affect hoarding behavior of related animals (e.g., Hadj-Chikh et al. 1996; Fleck and Woolfenden 1997; Steele, Smallwood, et al. 2001; Steele, Turner, et al. 2001; Steele et al. 2006; Xiao et al. 2008). Smallwood & Peters (1986) suggest that high tannins may provide a cue for tree squirrels to identify whether a given acorn is suited for hoarding or not. Because red oak acorns not only germinate later but also have higher tannin content compared with white oak acorns, the high-tannin hypothesis should also be true if red oak acorns are hoarded more than white oak ones as the food perishability hypothesis predicts (Fox 1982; Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele, Smallwood, et al. 2001; Steele, Turner, et al. 2001; Steele et al. 2006). Recent evidence from China provides field support for the high-tannin hypothesis that high-tannin acorns (i.e., *Q. variabilis*) are hoarded more than low-tannin ones (i.e., *Castanea henryi*) and also have a higher probability surviving as seedlings or long-term storage (Xiao et al. 2008; see also Wang and Chen 2008 using artificial seeds by adding different levels of tannins). More recently, we demonstrated that Pallas's squirrel (*Callosciurus erythraeus*) displayed embryo removal behavior to acorns from several Fagaceae species (e.g., *Castanea* spp., *Quercus* spp., and *Cyclobalanopsis* spp.) in the Qingcheng Mt in Dujiangyan City of Sichuan Province, Southwest China. In this study, our major goal is to investigate how Pallas's squirrels utilize acorns as long-term storage in response to both germination schedule and tannin levels in acorns.

Using acorns from *C. henryi* and *Q. variabilis* (Family Fagaceae) with contrasting germination schedule and tannin levels, we conducted field experiments in a subtropical forest in Southwest China to simultaneously test the food perishability and high-tannin hypotheses with free-ranging Pallas's squirrels (*C. erythraeus*). Here *Q. variabilis* nuts germinate much earlier than *C. henryi* ones (see Results), but the former have higher tannin level (10.7%) over the latter (0.6%) (see Xiao et al. 2008). Thus, we predicted that high-tannin *Q. variabilis* nuts are hoarded more (if the high-tannin hypothesis holds) or dormant *C. henryi* nuts are hoarded more (if the food perishability hypothesis holds). In addition, we also tested another 3 predictions derived from the food perishability hypothesis: 1) nondormant acorns (*Q. variabilis* here) are more likely to have their embryos removed (Fox 1982; Steele, Turner, et al. 2001); 2) embryo-removed acorns have a higher probability surviving as long-term food supply (Steele, Turner, et al. 2001); and 3) embryo-removed acorns have a lower probability to germinate (McEuen and Steele 2005). Contrary to the food perishability hypothesis, we also argued that embryo-removed acorns may not be good as long-term storage if they are more likely to be infested by fungi during the time of storage (up to several months). We also discussed behavioral adaptation in tree squirrels in response to germination schedule and tannin levels in acorns between China and North America.

## MATERIALS AND METHODS

### Study site and species

Field experiments were conducted in the Qingcheng Mt (1 national forest park) (900–1200 m, 31°03′N, 103°43′E) in Dujiangyan City of Sichuan Province, Southwest China. The vegetation is subtropical evergreen broad-leaved forest, where nut-bearing species such as Fagaceae species are most common. Two Fagaceae species, *C. henryi* and *Q. variabilis* were selected as experimental food items. Though nutrient contents such as starch, fat, and protein are much similar between the 2 nut species, tannin level and germination schedule were much different between them. *Quercus variabilis* nuts (11.7%; QV nuts, hereafter) have about 20 times the tannin level of *C. henryi* ones (0.6%; CH nuts, hereafter) (Xiao et al. 2003, 2008). As shown in the results, QV nuts germinated much earlier than CH ones, indicating that nondormant QV nuts are more perishable for hoarding and their embryos are more likely to be removed if they are used as long-term food supply. Due to some variation in seed mass between the 2 nut species, we only used nuts with fresh seed mass of 2.5–3.5 g.

Pallas's squirrel (*C. erythraeus*) is 1 tree squirrel species with body mass of approximately 250–400 g. They are distributed in Southern China and Southeast Asia and are also introduced in Japan and France (Xu and Ran 2004). Pallas's squirrels are found as important pests by gnawing barks and young shoots in many conifer plantations (e.g., Kuo and Liao 1986; Xu and Ran 2004; Tamura and Ohara 2005). Previous studies showed that Pallas's squirrels can hoard plant seeds during fruiting seasons in autumn (Chou et al. 1985; but see Setoguchi 1990). According to our recent and ongoing studies in Qingcheng Mt, this tree squirrel is a key scatter-hoarder for the dispersal of large seeds from Fagaceae species and other large-seeded species (e.g., *Camellia* spp.). The most exciting finding is that Pallas's squirrels remove acorn embryos from several Fagaceae species (e.g., *Castanea* spp., *Quercus* spp., and *Cyclobalanopsis* spp.), like *Sciurus* squirrels to white oak acorns reported in North America. Additionally, several other rodent species, for example, *Apodemus* spp. and *Niviventer* spp., were also trapped in Qingcheng Mt, but these rodents were found to not remove acorn embryos in a nearby forest named Banruosi Experimental Forest, approximately 20 km from the former forest (Xiao et al. 2003, 2008; Cheng et al. 2005; Chang et al. forthcoming).

### Hoarding experiment

CH nuts were collected from Qingcheng Mt, whereas QV nuts were collected from the nearby Banruosi Experimental Forest. Two hundred sound nuts were randomly selected for each nut species (total, 400) used for hoarding experiments, and they all showed no sign of germination (i.e., no radicle protruding from the pericarp) at the start of the experiment. Nuts were labeled with a numbered plastic tag attached by a thin stainless steel wire of 10 cm long (here plastic tags were used instead of tin tags, cf., Xiao et al. 2006). This method involves piercing the seed and thus has some damages on the cotyledons, but it is found to have no effect on the germination of large seeds such as *Q. variabilis* (Xiao et al. 2006). This seed-tagging method permits us to follow the exact fate and spatial pattern of caches over time until the seeds germinate and emerge as seedlings (Xiao et al. 2006).

On 13 October 2007, we established 10 successive plots as experimental seed stations along a transect and spaced 10–15 m apart and then placed 20 tagged nuts from each species at each seed station. Seed fate was monitored regularly with the intervals of 1–2 weeks until 25 December 2007. During each visit, we searched the area around each seed station (diameter: 10–30 m) to retrieve tagged nuts and record their fates. Nuts at each seed station were categorized as remaining, eaten, and removed, whereas tagged nuts after removed from seed stations were categorized as hoarded (i.e., buried in the surface soil or covered with leaf litter), eaten (marks and seed fragments found), or missing (not retrieved). For hoarded nuts, they were carefully excavated to identify whether their embryos were removed by animals, and then they were reburied to keep the disturbance to a minimum. Caching sites were marked using a numbered bamboo stick. At subsequent visits, we also checked the caches located in previous visits until they were recovered by animals. If a marked cache was removed, the area around the cache was haphazardly searched. On 25 March 2008, we also surveyed all previously cached sites to determine whether some of the cached nuts survived until germination (with taproots extending from nut apical).

### Germination experiment

In order to test whether embryo removal by animals affects seed germination and subsequent infestation by fungi, we randomly selected 120 CH nuts and 120 QV nuts, and then acorn embryos from half sample (60) were artificially removed for each species using drill by mimicking the animals' behavior. On 25 November 2007, these nuts were sowed under the surface soil with 2–4 cm depth like most rodent-made caches and watered regularly in experimental chambers. One month and 3 months after sowing, we carefully excavated 30 nuts for each treatment (i.e., embryos intact vs. removed) and each species, and these nuts were recorded whether they were germinated or not and then dissected to see whether embryo-removed nuts were more likely to be infested by fungi through embryo removal by animals.

### Statistical analysis

During the analysis, the following parameters are considered for the complicated fates of the tagged nuts: the time (week) to harvest (either eaten or removed) at the source, the proportions of nuts removed from the source, the proportions of nuts hoarded after removal (Hoarded-1), hoarded from Hoarded-1 (Hoarded-2), hoarded from Hoarded-2 (Hoarded-3), and final survival of the hoarded nuts from Hoarded-1, Hoarded-2, and Hoarded-3 on 25 March 2008. Hoarded nuts were further divided into 2 groups with embryos either remaining intact or removed by animals. Cox regression model was used to test the difference of the time to harvest (censored due to 3 QV nuts remaining intact at the source on 25 December 2007) between the 2 nut species. Because seed fate data are proportion data, logical regression models were used to test the differences between the 2 nut species. When overdispersion occurred in logistic regression models, we used family = quasibinomial instead of family = binomial (Crawley 2007). In germination experiments, Pearson chi-square tests or Fisher's Exact tests were used to test the difference in germination success or fungi infestation between 2 treatments (i.e., embryos intact vs. removed) for either each species or between species. All the analyses were carried out in R program (version 2.6.2, http://cran.r-project.org/).

## RESULTS

### Hoarding experiment

All CH nuts were harvested during the first 3 weeks, compared with only 68% of QV nuts (Wald = 170, degrees of freedom [df] = 1, $P < 0.0001$). CH and QV had as much as 97.5% and 92.5% of tagged nuts removed from the source, respectively, but the former species was removed more than the later species ($z = -2.009$, $P = 0.0445$) (Figure 1).

We relocated 79.0% and 91.4% of the tagged nuts after removed from the source for CH and QV, respectively. Most of the relocated nuts were cached singly (but 3 CH caches containing 2 nuts). The hoarding probability after removal (Hoarded-1) was significantly higher for QV nuts (77.3%) than CH nuts (64.1%) ($t = 2.847$, $P = 0.00446$) (Figure 1) This supports the high-tannin hypothesis that high-tannin nuts (QV here) are hoarded more than low-tannin ones (CH here) (Table 1). However, the hoarding probability from Hoarded-1 (i.e., Hoarded-2) and subsequent hoarding probability from Hoarded-2 (i.e., Hoarded-3) were not different between the 2 nut species (both $P > 0.5$) (Figure 1). Over 5 months after placement (25 March 2008), the final survival probability of the hoarded nuts (including Hoarded-1, Hoarded-2, and Hoarded-3) was significantly higher for QV (22.5%) than CH (11.5%) ($t = 2.565$, $P = 0.0109$) (Figure 1).

For nuts at Hoarded-1 stage, the probability of embryo-removed nuts increased over time for both nut species (Figure 2), but the embryo removal probability was significantly higher for QV (68.5%) than CH (8.8%) ($t = 8.407$, $P < 0.0001$) (Figure 1), supporting the prediction that nondormant nuts (QV here) are more likely to have their embryos removed. Acorn embryo removal probability at subsequent hoarding stages increased with up to 100% at Hoarded-3 stage, but no difference was found between the 2 nut species (both $P > 0.1$) (Figure 1). Over 5 months after placement (25 March 2008), the final survival probability of embryo-intact nuts was significantly lower than that of embryo-removed ones for both nut species (CH, 12.7% vs. 43.5%; QV, 24.3% vs. 34%) ($t = -3.364$, $P = 0.00134$) (Figure 1). This also supports the prediction that embryo-removed nuts have a higher survival probability as long-term food supply for hoarding animals.

### Germination experiment

One month (25 December 2007) and 3 months (25 February 2008) after sowing, we found that 32.0% and 85.7% of intact QV nuts germinated compared with 0% and 38.5% of embryo-removed ones, respectively (1 month, $P = 0.001$; 3 months, $\chi^2 = 12.908$, df = 1, $P < 0.001$) (Figure 3A,B). The same was also true for CH nuts (1 month, $P = 0.113$; 3 months, $\chi^2 = 17.912$, df = 1, $P < 0.001$) (Figure 3A,B). We also found that more intact QV nuts germinated than intact CH ones either 1 month ($\chi^2 = 6.241$, df = 1, $P = 0.012$) or 3 months ($\chi^2 = 1.697$, df = 1, $P = 0.193$) after sowing (Figure 3A,B). According to the field survey using the tagged nuts in hoarding experiments on 25 March 2008, all intact nuts germinated compared with 25% of embryo-removed CH nuts ($P = 0.001$) or 20% of embryo-removed QV nuts ($P < 0.001$) (Figure 3C). These results support the prediction that embryo-removed nuts have a lower probability to germinate.

One month or 3 months after sowing, however, very few intact or embryo-removed nuts (0–3 nuts out of 30 ones for each treatment) were infested by fungi for each nut species (the data were not presented here, all $P > 0.5$, Fisher's Exact test). On 25 March 2008, no fungi-infested nuts were found for each nut species regardless of their embryos either remaining intact or removed by animals according to the hoarding experiment. This suggests that most embryo-removed nuts were still alive for a much long time (up to 3–5 months here).

## DISCUSSION

We found that Pallas's squirrels could effectively use nondormant QV nuts as long-term storage. Similar to the studies from North America, our results provide clear evidence for several predictions derived from the food perishability hypothesis: 1) nondormant QV nuts had their embryos removed with a higher probability (68.5%) compared with late-germinating CH nuts (8.8%); 2) germination success was much lower for embryo-removed acorns than embryo-intact ones; and 3) embryo-removed acorns had a higher probability surviving as long-term food supply. Moreover, we also found that, during the caching-recovery process, hoarding animals actively detected acorn state (dormant or not) and removed acorn embryos with an

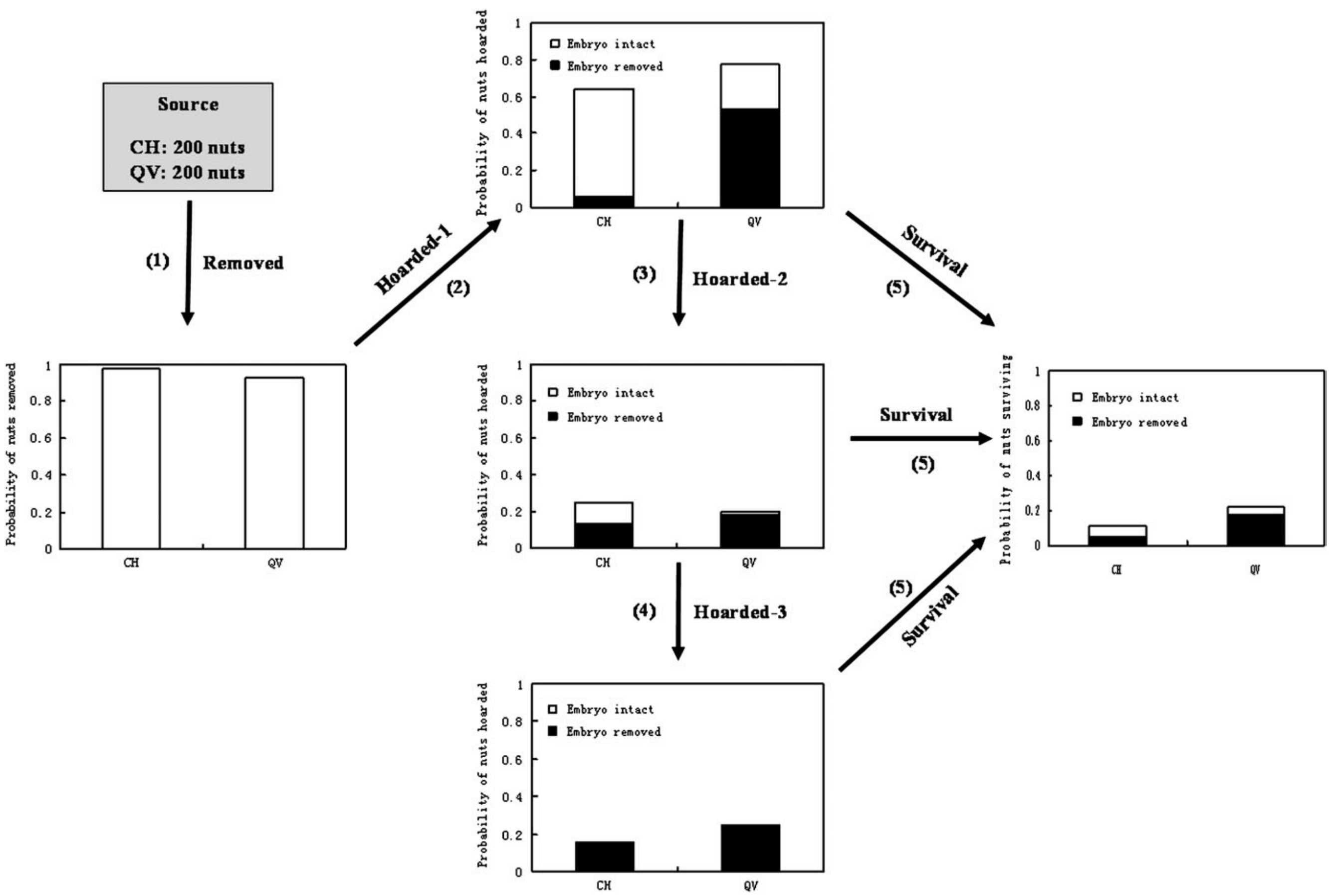


**Figure 1**
Survival probability of the tagged acorns with embryos either removed or intact at different hoarding stages for *Castanea henryi* (CH) and *Quercus variabilis* (QV): 1) removed from sources (removed), 2) hoarded after removal (Hoarded-1), 3) hoarded from Hoarded-1 (Hoarded-2), 4) hoarded from Hoarded-2 (Hoarded-3), and 5) final survival for all hoarded acorns from Hoarded-1, Hoarded-2, and Hoarded-3 on 25 March 2008 (survival).

increasing probability in subsequent hoarding events. In addition, we found that embryo-removed acorns could serve as long-term storage because they had a very low probability being infested by fungi as intact acorns did during the time of storage, which further supports the food perishability hypothesis. Thus, germination schedule may serve as a proximate cue for whether acorns have their embryos removed or not. However, we found that dormant CH nuts were less hoarded than nondormant QV nuts (see similar results in Xiao et al. 2008). Our result does not support the studies conducted in North America, which most hold the food perishability hypothesis (e.g., Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele, Smallwood, et al. 2001; Steele, Turner, et al. 2001; Steele et al. 2006). Thus, germination schedule here is not adequate to explain this inconsistence in hoarding patterns between our study and those in North America.

**Table 1**
**Hypotheses and predictions in relation to germination schedule (related to food perishability) and tannin level in acorns from *Quercus variabilis* and *Castanea henryi* (see text for details)**

| | Nut traits | | Predictions of alternative hypotheses | |
|---|---|---|---|---|
| Species | Germination schedule | Tannin level | Food perishability | Tannin |
| *Q. variabilis* | Early | High (11.7%) | Less | More |
| C. henryi | Late | Low (0.6%) | More | Less |

More, hoarded more; less, hoarded less. Shaded boxes indicate that predictions were most supported by our data.

In this study, we further confirm the high-tannin hypothesis because free-ranging Pallas's squirrels hoarded more high-tannin QV nuts though they harvested (either ate or hoarded) low-tannin CH ones more quickly (see also Xiao et al. 2008). Using artificial seeds by adding different levels of tannins, Wang and Chen (2008) also provide similar evidence for this hypothesis. Smallwood and Peters (1986) assumed that high tannins might serve as a proximate cue that squirrels use to recognize less perishable food (e.g., dormant acorns from red oaks) (see also Hadj-Chikh et al. 1996). However, tannin level and germination schedule in the 2 nut species used here were opposite to those in white oaks and red oaks used in North America. In this study, CH nuts had lower tannins but germinated later, whereas QV nuts had higher tannins but germinated earlier (Table 1). If Smallwood-Peters's assumption holds, the question is coming: nondormant QV nuts are not suitable for hoarding but high tannins indicate QV nuts suitable for hoarding. In this case, it is obvious that high tannins may not serve as a cue for tree squirrels to recognize less perishable food (here CH nuts). Evidence indicates that many hoarding animals such as squirrels, rats, and jays prefer to hoard more high-tannin acorns over low-tannin ones

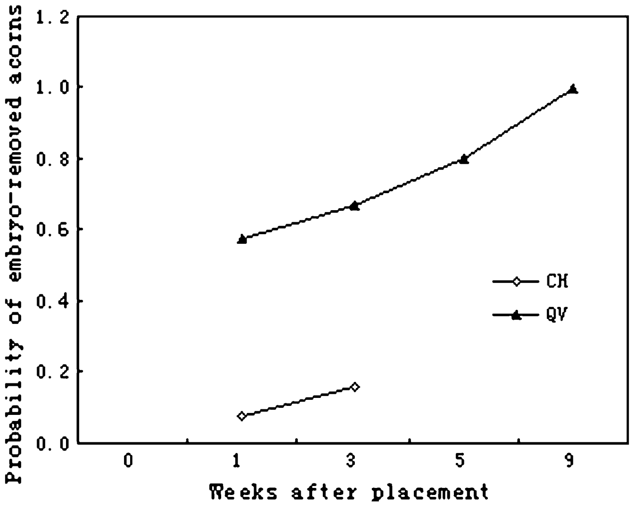


**Figure 2**
Temporal patterns of embryo-removed acorns when tagged acorns were removed and then hoarded by tree squirrels after placed at the sources. CH, *Castanea henryi*; QV, *Quercus variabilis*.

(e.g., Hadj-Chikh et al. 1996; Fleck and Woolfenden 1997; Steele, Smallwood, et al. 2001; Steele, Turner, et al. 2001; Steele et al. 2006; Xiao et al. 2008; this study). Other secondary compounds in nuts are also found to not influence hoarding behaviors by related animals, for example, quinolizidine alkaloids in *Ormosin arborea* seeds to agoutis (*Dasyprocta leporine*) (Guimarães et al. 2003). One potential reason why animals prefer to hoard more food with high level of secondary compounds (e.g., high-tannin acorns) is that secondary compounds such as tannins are expected to be degraded during storage (see Fleck and Woolfenden 1997). However, it is surprising that no evidence is found to support this prediction (e.g., Dixon et al. 1997; Koenig and Faeth 1998; Shimada 2001; Smallwood et al. 2001).

According to our study and those from North America, however, we found that tree squirrels from either China or North America hoard more high-tannin acorns than low-tannin ones though the studies from North America more emphasize that food perishability based on germination schedule is the determining factor. Because red oak acorns not only germinate later but also have higher tannin content (6–10%) compared with white oak acorns (e.g., Fox 1982; Hadj-Chikh et al. 1996; Smallwood et al. 2001), the high-tannin hypothesis should also be true if the food perishability hypothesis holds. In addition, red oak acorns also have higher fat content (ca., 20%), which may further enhance food value for hoarding animals (e.g., Smallwood and Peters 1986; Hadj-Chikh et al. 1996). However, tree squirrels do detect and response to germination schedule in acorns prior to hoarding. In this study, nondormant QV nuts may not be suitable for long-term storage, but their embryos are more likely to be removed than dormant CH ones, which could reduce energy loss through germination because germination success is much lower for embryo-removed acorns (see Results). Thus, embryo removal by tree squirrels is extremely important if nondormant acorns were used as long-term storage as did in this study and others (e.g., Steele, Turner, et al. 2001; see also Jansen et al. 2006). In addition, the food perishability hypothesis does work efficiently if germination schedule is the key factor between the acorns sampled by hoarding animals, for example, germinating versus nongerminating acorns from the same oak species (e.g., Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2006; Chang et al. forthcoming).

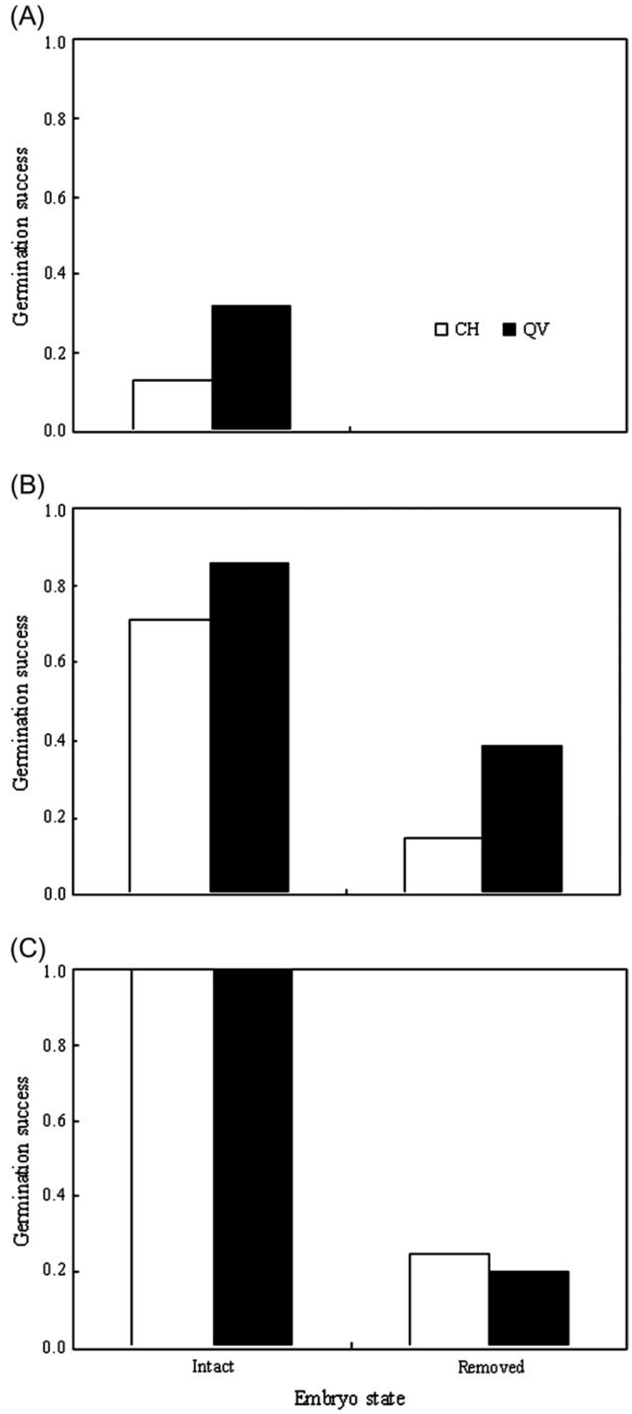


**Figure 3**
Germination success of buried acorns of *Castanea henryi* (CH) and *Quercus variabilis* (QV). (A and B) 1 and 3 months after sowed the acorns with embryos remaining intact or artificially removed on 25 November 2007, respectively, and (C) rodent-made caches from the tagged acorns in hoarding experiment on 25 March 2008 (over 5 months).

To conclude, we have shown how tree squirrels (Pallas's squirrels here) manage their caches as long-term food supply in response to both germination schedule and tannin levels in acorns. We found that tree squirrels can differentially respond to acorn germination and remove the embryos of nondormant acorns more frequently as long-term storage, but acorn tannin level is more important in determining whether a given acorn is hoarded or not. Though there are substantial differences in the animal and acorn assemblages between China and North America, our new record on acorn embryo removal behavior by Pallas's squirrels in China provides significant evidence that the evolution of acorn embryo removal behavior in tree squirrels is a counteradaptation to deal with nondormant phenotype in white oaks worldwide. Combined with the studies from North America, our results suggest convergent evolution of acorn hoarding behavior in tree squirrels across different continents. Further investigations are required to reveal the adaptive convergence of squirrels' hoarding behavior and its underlying selection to the evolution of seed traits among oak species and other seed species across continents.

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