



Testing the high-tannin hypothesis with scatter-hoarding rodents: experimental and field evidence

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(Received 1 May 2007; initial acceptance 20 July 2007;
final acceptance 23 August 2007; published online 20 February 2008; MS. number: 9379)

With a combination of both experimental (caged, hours/daily) and field (free-ranging, several months) studies, we tested the high-tannin hypothesis that hoarding animals prefer to eat more low-tannin food items immediately but hoard more high-tannin items for later consumption. We studied two common rat species (Edward's long-tailed rat, *Leopoldamys edwardsi*; and chestnut rat, *Niviventer fulvescens*) and two nut species (Henry's chestnut, *Castanea henryi*; and cork oak, *Quercus variabilis*) that show varying tannin levels (0.6% versus 11.7%) but are similar in other traits. Based on the high-tannin hypothesis, we predicted that (1) both rat species would eat more low-tannin *C. henryi* nuts instantly but fewer high-tannin *Q. variabilis* nuts and (2) after harvesting a given nut, they would prefer to hoard more *Q. variabilis* nuts and fewer *C. henryi* nuts. The first prediction was firmly supported in our study: both rat species ate more *C. henryi* nuts than *Q. variabilis* nuts under all conditions. However, the second prediction was supported only in the field study, which lasted over several months, in contrast to the experiments conducted in seminatural enclosures (only 1 day). We found that high-tannin *Q. variabilis* nuts, in contrast to low-tannin *C. henryi* nuts, had a significantly higher probability of being hoarded and surviving as seedlings in the field. We conclude that experimental conditions used here are less likely to result in natural feeding preferences of tested animals and the high-tannin hypothesis is supported especially in the field setting.

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Keywords: chestnut rats; Edward's long-tailed rats; food preference; *Leopoldamys edwardsi*; *Niviventer fulvescens*; scatter hoarding; tannins

Many birds and rodents scatter hoard nuts in surface soil for later use (Smith & Reichman 1984; Vander Wall 1990), and scatter hoarding is a key means of seed dispersal for many nut-bearing plants (Vander Wall 2001). An important issue in the study of the evolutionary interactions between scatter-hoarding animals and plant seeds is to determine how reciprocal selection pressures influence the evolution of morphological, physiological, chemical and behavioural traits (Smith & Reichman 1984; Vander Wall 1990). The behavioural decision of what to eat or hoard is extremely important for the survival and reproductive success of hoarding animals. Thus, most scatter-hoarding animals should have evolved some mechanisms to choose and eat or hoard a given food item when encountered: the more efficient such decisions are, the

more likely a species is to survive and reproduce (Smith & Reichman 1984; Vander Wall 1990). However, seed traits such as seed value and physical and chemical defences can significantly influence such decisions. For example, high-value seeds such as larger seeds are more likely hoarded and dispersed farther (Stapanian & Smith 1978, 1984; Smith & Reichman 1984), nuts with hard hulls are hoarded more due to longer handling time (e.g. Jacobs 1992; Xiao et al. 2003) and secondary compounds in nuts could deter feeding but not hoarding in foraging animals, for example, quinolizidine alkaloids in *Ormosin arborea* seeds eaten by agoutis, *Dasyprocta leporina* (Guimarães et al. 2003).

Tannins, a group of phenolic compounds common in nuts, are believed to be chemical deterrents used to defend against insect and vertebrate seed predators because of their negative effects such as interference in digestion, reduction in food palatability, failure of kidney or liver, loss of body weight, loss of endogenous nitrogen or even

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death (Vander Wall 2001; Shimada & Saitoh 2006; and references therein). The oaks, *Quercus*, are well known to produce nuts with considerable variation in tannin content. For example, acorns of red oaks, subgenus *Erythrobalanus*, often have higher tannin content (6–10%) whereas acorns of white oaks, subgenus *Quercus*, often have lower tannin content (0.5–2.5%; e.g. Smallwood & Peters 1986; Steele et al. 1993; Smallwood et al. 2001; Vander Wall 2001). Moreover, the tannins in nuts could affect feeding and hoarding preferences of many animals. However, the effects of nut tannins on feeding and hoarding preferences have been debated for a long time: some believe that animals prefer red oak acorns over white oak acorns with an emphasis on high fat content in red oak acorns (Smith & Follmer 1972; Lewis 1980, 1982), whereas others hold that animals prefer to feed on low-tannin white oak acorns over high-tannin red oak acorns (Short & Epps 1976; Smallwood & Peters 1986; Smallwood et al. 2001). The contrasting views may result mainly from different experimental conditions (caged versus free-ranging animals), covarying seed traits such as tannin, fat and others (e.g. germination schedule) among different nut types and seasonal changes in behaviours and physiological requirements of testing animals (see also Smallwood & Peters 1986). Smallwood & Peters (1986) attempted to resolve the controversy by using the acorns of *Quercus alba* (one white oak) as artificial acorn material. After adding different amounts of tannin and fat, they found that in autumn grey squirrels, *Sciurus carolinensis*, spent more time feeding on low-tannin food items while in winter the squirrels selectively consumed food items with higher lipid levels to meet energy requirements even when they contained higher tannin levels.

Smallwood & Peters (1986) also reasoned that hoarding animals prefer to hoard more high-tannin food for later consumption (i.e. the high-tannin hypothesis; see also Fleck & Woolfenden 1997). Specifically, they hypothesized that high tannins were a proximate cue that squirrels use to recognize less-perishable food, which is more suited to storage. So far, only a few animal species mostly from Northern America, for example grey squirrels (e.g. Smallwood & Peters 1986; Hadj-Chikh et al. 1996; Steele et al. 1996; Smallwood et al. 2001) and scrub jays, *Aphelocoma coerulescens* (Fleck & Woolfenden 1997), have been used to test the high-tannin hypothesis. However, evidence from Northern America suggests that food perishability (i.e. germination schedule) rather than tannin levels may directly influence hoarding behaviour: acorns of red oaks with delayed germination are found hoarded more than those of white oaks (e.g. Hadj-Chikh et al. 1996; Steele et al. 1996; Smallwood et al. 2001; but see Fleck & Woolfenden 1997). This appears to dispute the high-tannin hypothesis. In these studies, however, acorns of white oaks and red oaks used also covary in fat content and germination schedule, not just tannins (Hadj-Chikh et al. 1996; Steele et al. 1996; Smallwood et al. 2001). Therefore, it is critical to control other seed traits when considering the effects of tannins.

In this study, we further tested the high-tannin hypothesis using two common rat species (Edward's long-tailed rats, *Leopoldamys edwardsi*; and chestnut rats, *Niviventer*

fulvescens) and two nut species (Henry's chestnut, *Castanea henryi*; and cork oak, *Quercus variabilis*) that show varying tannin levels (0.6% versus 11.7%) but are similar in other traits. We conducted experiments under both experimental and field conditions in a subtropical forest: Banruosi Experimental Forest, Southwest China. The combination of both experimental (caged, hours/daily) and field (free-ranging, several months) conditions allowed us to elucidate the extent to which several environmental factors (e.g. cage and time) could affect food preference observed in previous studies. This is also essential for precisely assessing food preference in relation to main factors (here, tannin). Based on the high-tannin hypothesis, we predicted that (1) both rat species would eat more low-tannin *C. henryi* nuts instantly and fewer high-tannin *Q. variabilis* nuts and (2) after harvesting a given nut, they would prefer to hoard more *Q. variabilis* nuts and fewer *C. henryi* nuts.

METHODS

Study Site and Species

We conducted three experiments in the Banruosi Experimental Forest (700–1000 m, 31°4'N, 103°43'E) in Dujiangyan City of Sichuan Province, Southwest China. The vegetation is subtropical evergreen broadleaved forests, where nut-bearing species such as Fagaceae species are most common. Two nut species, *Q. variabilis* and *C. henryi*, were selected as experimental food items. *Quercus variabilis* nuts were collected from the Banruosi Experimental Forest, and *C. henryi* nuts were collected from a nearby forest, Qingcheng Mt. (one national forest park), ca. 20 km from the Banruosi forest. These two nut species have similar seed masses (mean, ca. 2.5 g) and nutrient contents (e.g. starch, fat and protein) but differ mainly in tannin content (Table 1). *Quercus variabilis* nuts have a high tannin concentration (11.68%) compared to the low tannin content (0.57%) in *C. henryi*

Table 1. Nut properties of *Quercus variabilis* and *Castanea henryi*

Description	<i>Quercus variabilis</i>	<i>Castanea henryi</i>
Fresh mass (mean±1 SD g, N=30)	2.56±0.14	2.50±0.11
Crude starch (% of dry nutmeat)	54.17	58.71
Crude protein (% of dry nutmeat)	5.92	7.05
Crude fat (% of dry nutmeat)	3.94	1.11
Tannin (% of dry nutmeat)	11.68	0.57
Crude fibre (% of dry nutmeat)	2.87	2.31
Ash (% of dry nutmeat)	2.35	2.59
Caloric value (per gram of dry nutmeat)	17.63	16.58

Data of chemical compositions (i.e. crude starch, crude protein, crude fat, tannin and crude fibre) of dry nutmeat were provided by the Centre of Grain Quality of Ministry of Agriculture, China, and caloric value of dry nutmeat was measured by Bomb Calorimetre (PARR 1281) in the Institute of Zoology, CAS.

nuts. Due to variation in seed mass among individual nuts for both nut species, we used only nuts with fresh seed mass of 2.1–2.5 g. For experiments in mouse cages and seminatural enclosures, germinating *Q. variabilis* nuts were also discarded regardless of seed mass because germinating nuts may be perceived as more perishable and thus have less value for hoarding by rodents (see Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001a, b, 2006). In field experiments, however, it was difficult to control for seed germination since the experiments lasted several months. Unlike the studies discussed above, both *C. henryi* and *Q. variabilis* nuts germinated during the field experiment, but the oak germinated sooner (Z. Xiao, personal observation). Our previous studies indicate that germinating nuts such as *Q. variabilis* have little effect on feeding and hoarding by rodents, and they are found cached with their taproots cut but embryos not excised (Z. Xiao, personal observation).

Two common rat species with high abundance were used in this study: Edward's long-tailed rats and chestnut rats. To trap the animals we used large wired cage traps (30 × 25 × 20 cm) of our own design approved by the Institute of Zoology, CAS baited with peanuts and small pieces of cabbage, water and local dry leaves as nest materials in the Banruosi Experimental Forest. Traps were placed at 0700–0730 hours and checked after 12 h, and all captured animals were healthy when checked. The animals in reproductive conditions were released immediately on site. Before experiments, all animals were kept individually in a large mouse cage (50 × 30 × 25 cm) with adequate laboratory chow, water and nest structures under room temperature (10–15°C) and natural photoperiod (ca. 12:12 h light:dark cycle). During captive experiments, adequate water and nest structures were always provided ad libitum. After experiments, all animals were released where they were captured. Edward's long-tailed rats are large rats (ca. 200–500 g), whereas chestnut rats are relatively small (<100 g). Our previous and ongoing studies have shown that Edward's long-tailed rats are principal scatter hoarders for several large-seeded plants, but chestnut rats are found hoarding fewer nuts (Xiao et al. 2003, 2005, 2006a; Cheng et al. 2005). Both field and experimental observations showed that these rodents displayed significant differences when eating and/or hoarding several nut species (Xiao et al. 2003, 2005, 2006a; Cheng et al. 2005; unpublished data). However, it is not clear how tannins in nuts affect feeding and hoarding preferences for a given rodent species when controlling for other seed traits.

Feeding Experiments in Cages

Ten individuals of each rat species (five males and five females) were used to investigate feeding preferences of nuts during late October and early November 2005. All animals were held individually in a large mouse cage (50 × 30 × 25 cm). Before experiments, we provided some nuts of *C. henryi* and *Q. variabilis* as food for testing animals because the captured animals may have had previous experience with *Q. variabilis* nuts but not those of *C. henryi*. We first conducted preliminary experiments to

determine how many nuts of either *C. henryi* or *Q. variabilis* were consumed by one animal within 12–14 h (only Edward's long-tailed rats were used). We found that ca. 20 nuts of each species were enough for overnight feeding (12–14 h) even though Edward's long-tailed rats were larger rats. During the regular experiments, we provided 10 nuts of each species to each individual of both rat species. The feeding bout lasted only 4 h for each animal (from 1800 to 2400 hours), which was tested only once. Then we collected all the nuts and nut fragments to determine how many nuts were sampled (gnawed) by the animal. A gnawed nut was defined as any nut for which over 5% of the total mass was consumed.

Feeding and Hoarding Experiments in Seminatural Enclosures

Experiments were conducted in four 10 × 10-m seminatural enclosures (see Cheng et al. 2005 for details) during November and December 2005. For each rodent species, eight individuals (four female and four male) were tested for a one-night bout of hoarding. Before the experiments, each animal was introduced into the enclosure to move freely for one night. During each bout, 20 nuts for each species with small coded plastic tags were placed at the centre of each enclosure at 1730 hours. Each bout lasted ca. 14 h from 1730 to 0730 hours. After removing the animal, we searched for the target nuts or nut fragments and recorded their fates (i.e. eaten or hoarded). Hoarded nuts were buried alone or in pairs in the soil (0–5 cm); nuts placed on the soil surface were not included in the analysis although they were carried some distances away from the food pile.

Feeding and Hoarding Experiments in the Field

We labelled 100 nuts of each species with numbered plastic tags attached by 10-cm-long thin stainless steel wires (here plastic tags were used instead of tin tags, cf. Xiao et al. 2006b). This method involves piercing the seed, which damages the cotyledons and thus may reduce seed germination but does no more damage than the commonly used method of thread-marking (Xiao et al. 2006b). 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 (e.g. Xiao et al. 2005, 2006b).

On 14 October 2005, 10 tagged nuts per species were placed on the ground within 1 m² at 10 feeding stations along a transect, with 10–15 m between neighbouring stations. Seed fate was monitored regularly at intervals of 2–8 days until 7 December 2005. During each visit, we searched the area around each feeding station (diameter: 10–30 m) to retrieve removed nuts and record their fates. Nuts at each feeding station were categorized as remaining, eaten or removed; removed nuts were further categorized as cached (i.e. buried in the surface soil or covered with leaf litter), eaten (marks and seed fragments found) or missing (not retrieved). Caching sites were marked

using a numbered bamboo stick (15 × 1.5 cm). At subsequent visits, we also checked the caches located in previous visits until they were recovered by rodents. If a marked cache was removed, the area around the cache was haphazardly searched. On 6 May 2006, we also surveyed all previously found cache sites to determine whether some of the cached nuts survived until germination or seedling emergence.

Statistical Analysis

For experiments under cage and seminatural enclosure conditions, data on nuts eaten, harvested or hoarded were proportion data and were transformed using the arcsine square-root method. Paired *t* tests were used to test the differences in feeding or hoarding preferences in the two nut species when the variances were equal; otherwise Wilcoxon signed-ranks tests were used. For the field experiment, seed fate data were pooled for all feeding stations, and Pearson's chi-square tests or Fisher's exact tests were used to test the differences in seed fate in the two nut species. A Cox regression model was also used to test the difference in nuts surviving at feeding stations in the two nut species. All statistical tests were two tailed.

RESULTS

Feeding Preference in Cages

During the 4-hour feeding bouts in cages, both Edward's long-tailed rats and chestnut rats ate significantly more low-tannin *C. henryi* nuts (92 and 71%, respectively) than high-tannin *Q. variabilis* nuts (<40%) (Edward's long-tailed rats: $Z = 2.527$, $N = 10$, $P = 0.012$; chestnut rats: $t_9 = 3.1616$, $P = 0.012$; Fig. 1).

Feeding and Hoarding Preference in Seminatural Enclosures

During each bout, Edward's long-tailed rats harvested over 91% of the provided *C. henryi* nuts compared with

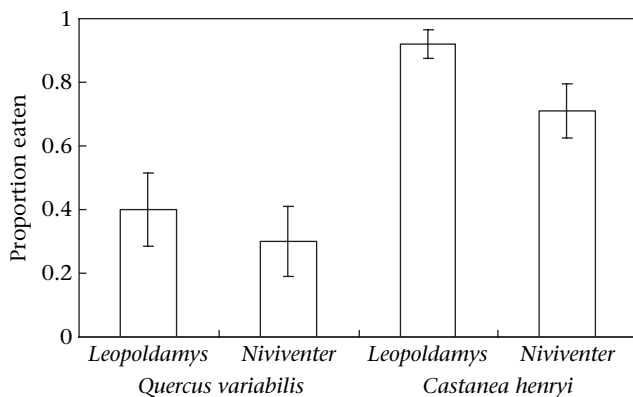


Figure 1. Feeding preference (mean ± SE, $N = 10$) between high-tannin *Quercus variabilis* and low-tannin *Castanea henryi* nuts by rats *Leopoldamys edwardsi* and *Niviventer fulvescens*.

15% of the *Q. variabilis* nuts ($t_7 = 9.607$, $P < 0.001$; Fig. 2). After harvest, Edward's long-tailed rats also hoarded 42% of *C. henryi* nuts but only 20% of *Q. variabilis* nuts ($Z = 1.524$, $N = 8$, $P = 0.128$; Fig. 2).

Similar to Edward's long-tailed rats, chestnut rats also harvested a high proportion (ca. 80%) of *C. henryi* nuts but an extremely low proportion (only 3%) of *Q. variabilis* nuts ($Z = 2.527$, $N = 8$, $P = 0.012$; Fig. 2). Chestnut rats also hoarded more *C. henryi* nuts (ca. 29%) than *Q. variabilis* nuts (0%) ($Z = 2.521$, $N = 8$, $P = 0.012$; Fig. 2).

Feeding and Hoarding Preference in the Field

Castanea henryi nuts were harvested much faster than *Q. variabilis* nuts (Cox regression model: Wald = 82.286, $P < 0.001$; Fig. 3). About one quarter of *Q. variabilis* nuts remained intact at feeding stations over about 2 months (54 days) after placement, whereas all *C. henryi* nuts were harvested within 10 days (mean ± SD: 3.7 ± 1.9 days; Fig. 3).

Castanea henryi nuts were eaten significantly more frequently but removed less frequently than *Q. variabilis* nuts at feeding stations ($\chi^2 = 7.091$, $P = 0.008$). However, *Q. variabilis* nuts were hoarded more in primary caches than *C. henryi* nuts after removal (56.25% versus 19.46%; $\chi^2 = 22.258$, $P < 0.001$) and more in secondary caches (15.56% versus 9.09%) ($P = 0.503$; Fig. 4). For cached nuts, 8% of the *Q. variabilis* nuts survived to germinate or even emerge as a seedling the following May, in contrast to 0% for *C. henryi* ($P = 0.007$).

DISCUSSION

With the combination of both captive and field experiments, we found that Edward's long-tailed rats and chestnut rats displayed similar feeding and caching responses to these nuts. Under captive experimental conditions, both rat species ate and/or hoarded more low-tannin *C. henryi* nuts than high-tannin *Q. variabilis* nuts. However, free-ranging animals ate significantly more *C. henryi* nuts but hoarded more *Q. variabilis* nuts. According to the high-tannin hypothesis, our first

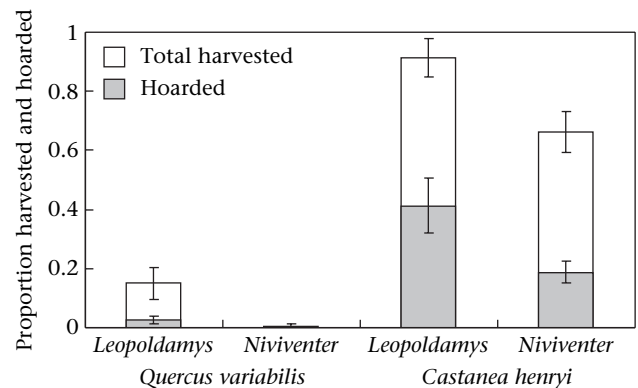


Figure 2. Differences in proportion harvested and hoarded (mean ± SE, $N = 8$) between *Quercus variabilis* and *Castanea henryi* nuts by rats *Leopoldamys edwardsi* and *Niviventer fulvescens*.

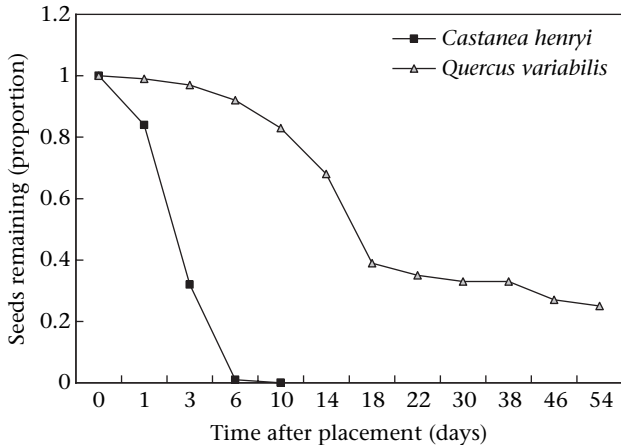


Figure 3. Survival curve (proportion) of 100 tagged nuts after placement at feeding stations for each of two nut species with contrasting tannin levels: *Castanea henryi* (0.6%) and *Quercus variabilis* (11.7%).

prediction is firmly supported, but our second prediction is supported only in the field experiments, which lasted over several months, in contrast to the experiments in seminatural enclosures (only 1 day). This is the first study to show that chestnut rats scatter hoard *C. henryi* nuts (but not *Q. variabilis* nuts) although not as readily as Edward's long-tailed rats (but see Cheng et al. 2005). Our results have three important implications for elucidating food preference in the context of the high-tannin hypothesis.

First, our controlled experimental conditions may influence hoarding behaviour more than feeding behaviour. Obviously, animals may behave differently when caged,

but our study found differences only in their hoarding behaviour and not in their feeding preferences. In the field, many factors may affect the hoarding and foraging behaviours of animals (Vander Wall 1990): food quantity and quality, predation risk, competition, and environmental conditions (e.g. weather). In this study, tannins in nuts significantly deter feeding of testing animals (see Results), but hoarding preferences for high-tannin *Q. variabilis* nuts in seminatural enclosures may be masked by our short observation period (only 1 day).

Second, tannins in nuts are most important to deter feeding by foraging animals. Under both experimental and field conditions, both rat species consume more low-tannin *C. henryi* nuts than high-tannin *Q. variabilis* nuts. If everything else is equal, high tannin levels could largely determine whether nuts are consumed because tannins in nuts can lead to many physiological deficiencies or even death of foraging animals (Vander Wall 2001; Shimada & Saitoh 2006). In this study, *Q. variabilis* nuts have about 20 times the tannin level of *C. henryi* nuts, whereas *C. henryi* nuts are sweet and thus more preferred by feeding animals (including humans). Our results also confirm most of the previous observations under either experimental or field conditions. For example, white oak acorns with lower tannins (0.5–2.5%), in contrast to high-tannin acorns from red oaks, are also preferred by either caged grey squirrels (Short & Epps 1976; but see Smith & Follmer 1972) or free-ranging squirrels (Smallwood & Peters 1986; Hadj-Chikh et al. 1996; Smallwood et al. 2001; but see Lewis 1980, 1982). Other animals, e.g. white-footed mice, *Peromyscus leucopus* (Briggs & Smith 1989), and eastern chipmunks, *Tamias striatus* (Pyare et al. 1993), are also found

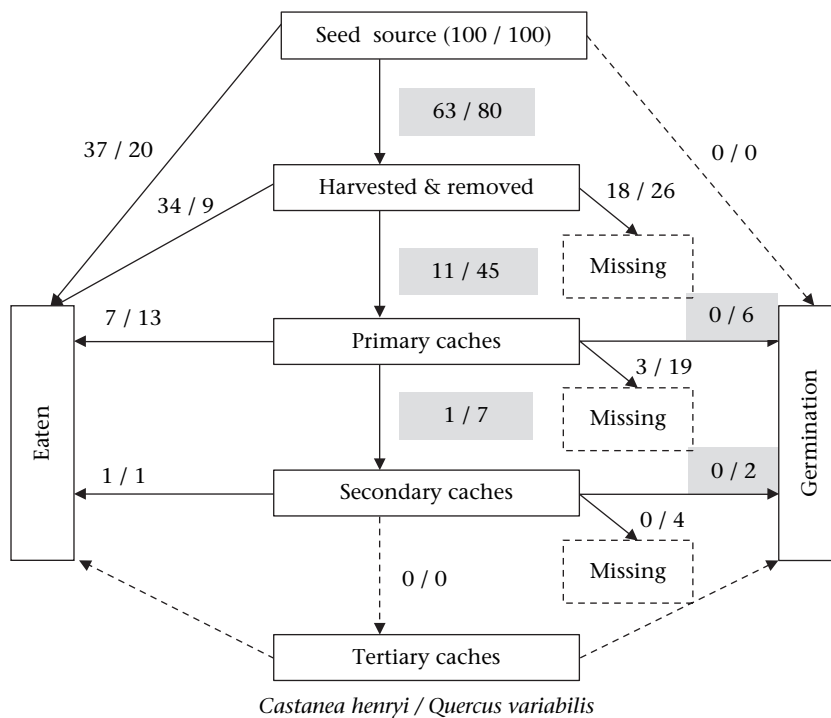


Figure 4. Fate pathways of 100 tagged nuts after placement at feeding stations for each of two nut species with contrasting tannin levels: *Castanea henryi* (0.6%) and *Quercus variabilis* (11.7%). The numbers of nuts harvested, re-/cached and surviving in next spring are shadowed.

to show similar feeding preferences for white oak acorns. Thus, feeding preference for low-tannin food by animals may be common across different geographical regions.

Third, it is hard to determine how nut tannins affect hoarding preferences, although our study showed that the high-tannin hypothesis is supported in the field setting. Our results indicate that high-tannin nut species could have high probabilities of seed dispersal success if high tannins in nuts deter feeding but not hoarding by related animals. However, it is not clear why rats prefer to hoard more high-tannin *Q. variabilis* nuts because in our system these nuts germinate early (in contrast to the high-tannin acorns in North American studies; see Introduction). Perhaps low tannins here may correlate with some other aspects of perishability (e.g. higher insect infestation rates, as in Smallwood et al. 2001). Another possible reason is that low-tannin nuts were limited, and there were no other choices for these rodents in the study site. Contrary to this study, we also found that free-ranging rock squirrels, *Sciurotamias davidianus*, prefer to hoard more low-tannin *C. henryi* nuts than high-tannin *Q. variabilis* nuts in Qingcheng Mt., where the *C. henryi* population is large but the *Q. variabilis* population is extremely small (only a few individuals; Z. Xiao, unpublished data). In addition, the negative effects of tannins may be reduced if they are stored for a longer time (see Fleck & Woolfenden 1997). However, this pattern has not been found in several studies (e.g. Dixon et al. 1997; Koenig & Faeth 1998; Shimada 2001; Smallwood et al. 2001). If *Q. variabilis* nuts are hoarded for a long time (e.g. several months here), they definitely could escape predation by germinating and emerging as seedlings because they germinate very readily.

In the field, it is possible that low-tannin *C. henryi* nuts are used first, either eaten or hoarded as shown in the seminatural enclosures, and *Q. variabilis* nuts are used much later because of high tannin levels. Foraging animals could switch their physiological requirements as seasons change and thus change their foraging behaviours accordingly. For instance, grey squirrels prefer more high-fat food during cold winter months even if it contains higher tannin levels, whereas these squirrels prefer more low-tannin food in the autumn (Smallwood & Peters 1986). Commonly, seed traits covary among co-occurring species. For example, fat content and germination schedule covary with tannin levels in the acorns of oak species in North America. Acorns of red oaks have higher fat content (18–25%), higher tannin content (6–10%) and delayed germination, but those of white oaks have lower fat content (5–10%), lower tannin content (0.5–2.5%) and early germination (Smallwood & Peters 1986; Smallwood et al. 2001; Steele et al. 2001a; Vander Wall 2001). However, food perishability (i.e. germination schedule) rather than tannin levels largely affects hoarding preferences (e.g. Hadj-Chikh et al. 1996; Steele et al. 1996; Smallwood et al. 2001; but see Fleck & Woolfenden 1997). In North America, several squirrel species may even have evolved adaptive strategies to excise the embryos of white oak acorns when dealing with their early germination (Fox 1982; Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2001a, b, 2006), but this phenomenon is not found in other rodents especially in Asia

and Europe, where many white oaks occur. In this study, *Q. variabilis* nuts, germinating a little earlier than *C. henryi* nuts, may be hoarded less but eaten more if germinating nuts are more perishable (food perishability hypothesis; see also Hadj-Chikh et al. 1996; Steele et al. 1996, 2001a, b, 2004, 2006). However, our results, in contrast to those from Northern America, indicate that tannins in nuts rather than early germination would largely affect feeding and hoarding preference. Thus, there may be some divergence in hoarding preference in response to tannin levels for related animals in this study and those conducted in North America.

In conclusion, our study supports the high-tannin hypothesis especially in the field setting. With the combination of both captive and field experiments, we found that experimental conditions used here are less likely to result in natural feeding preferences of tested animals and nut tannins are powerful at preventing consumption, but the extent to which tannins could determine hoarding may be dependant upon other factors. We also found that high-tannin *Q. variabilis* nuts, in contrast to low-tannin *C. henryi* nuts, have a significantly higher probability to be hoarded and then survive as seedlings in the field. In many forests like our study site, many nut-bearing species (e.g. Fagaceae species) co-occur within one community, and their seed traits covary in many ways, e.g. seed size, nutrient quality, nut hull, tannin content and germination schedule. Thus, further studies are needed to elucidate how these covarying seed traits, including tannins, interact to influence food preference of target animals.

Acknowledgments

We are very grateful to Mike A. Steele, Lixin Sun and two anonymous referees for valuable comments and suggestions on the early manuscript drafts. We also thank the Subalpine Mountain Plant Garden of West-China, CAS and the Forest Bureau of Dujiangyan City of Sichuan Province for support. Field assistance was provided by Li Bo and Cao Lin. Funds were provided by the National Natural Science Foundation of China (30430130 and 30500072), the Key Project of Ministry of Science and Technology (2005BA529A05) and the CAS Innovative Research International Partnership Project (CXTDS2005-4).

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