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

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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.

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	*Quercus variabilis*	*Castanea henryi*
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.