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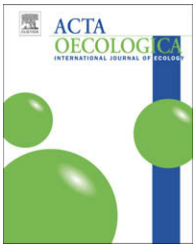

Original article

Tannin concentration enhances seed caching by scatter-hoarding rodents: An experiment using artificial 'seeds'

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ABSTRACT

Tannins are very common among plant seeds but their effects on the fate of seeds, for example, via mediation of the feeding preferences of scatter-hoarding rodents, are poorly understood. In this study, we created a series of artificial 'seeds' that only differed in tannin concentration and the type of tannin, and placed them in a pine forest in the Shangri-La Alpine Botanical Garden, Yunnan Province of China. Two rodent species (*Apodemus latronum* and *A. chevrieri*) showed significant preferences for 'seeds' with different tannin concentrations. A significantly higher proportion of seeds with low tannin concentration were consumed *in situ* compared with seeds with a higher tannin concentration. Meanwhile, the tannin concentration was significantly positively correlated with the proportion of seeds cached. The different types of tannin (hydrolysable tannin *vs* condensed tannin) did not differ significantly in their effect on the proportion of seeds eaten *in situ vs* seeds cached. Tannin concentrations had no significant effect on the distance that cached seeds were carried, which suggests that rodents may respond to different seed traits in deciding whether or not to cache seeds and how far they will transport seeds.

1. Introduction

Scatter-hoarding rodents can play an important role in the seed-to-seedling phase of plants, both as consumers and as dispersers of seeds (Price and Jenkins, 1986; Vander wall, 1990). The advantages of seeds being transported away from the parent trees and buried in the topsoil over a large surface can outweigh the disadvantage of a percentage of seeds being eaten during the caching process or during the later use of the caches (Hoshizaki et al., 1999; Theimer, 2001; Vander Wall, 2001). When a rodent encounters a seed and decides to consume it, the animal usually has two choices: eat the seed *in situ* or carry it to another place. The latter action often helps seeds escape further predation. Therefore, rodent behaviors and preferences for seeds often indicate differences in a seed's fate (Lima et al., 1985).

Innate seed traits such as size, nutritional quality, morphological and chemical defensive features, can influence the preferences of rodents, thus affecting seed survival and seedling recruitment (Vander wall, 1990; Forget et al., 1998; Brewer, 2001; Jansen et al., 2004; Xiao et al., 2006). Many studies have suggested that rodents often prefer to transport and cache larger seeds or seeds with higher fat content, compared with seeds eaten *in situ* (Vander Wall, 1995, 2003; Forget et al., 1998; Jansen and Forget, 2001; Jansen et al., 2004; Xiao et al., 2006). Seeds with harder seed hulls had higher rates of seed

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removal and reduced rates of instant consumption compared with seeds with softer hulls (Hadj-Chikh et al., 1996; Zhang et al., 2005). Toxicity of seeds may also reduce animal feeding preferences (Janzen, 1969; Kollmann et al., 1998).

Numerous nut-bearing plants appear to discourage nut consumption by producing nuts with large concentrations of phenolic compounds. However, there are relatively few studies of the effects of tannin concentration upon seed fates, and the existing studies often show paradoxical results. Some studies found that rodents preferred to eat some kinds of acorns with low tannin content and cache acorns with high tannin content (Wecherly et al., 1989; Shimada, 2001a; Smallwood et al., 2001; Wood, 2005). Nevertheless, Xiao et al. (2006) found that seeds with higher tannin concentration had lower probability of being transported and higher probability of being instantly consumed than some other seeds with low tannin concentration. The seemingly contradictory pattern for the effect of tannin content on seed fate may also be due to the methods adopted by researchers. Most of these studies used different species, and interspecific comparisons of the effect of tannins were often confounded by other characteristics of seeds.

A number of studies have used artificial foodstuff/diets to understand animal behavioral response to changes of food quality by adding a single nutrient or defensive compounds (Smallwood and Peters, 1986; Lewis et al., 2001; Downs et al., 2003; Bergvall and Leimar, 2005). This method could overcome the disadvantage mentioned above for real food items, often with several associated characteristics. To the best of our knowledge, there has so far been no test of the effect of tannin concentration on food preferences of scatter-hoarding rodents using this method.

The most important phenolic compounds in plants are hydrolysable and condensed tannins. The role of tannins in plant tissue is often controversial, perhaps because tannins are highly variable in chemical structure and have different effects in different situations (Vander Wall, 2001). Both hydrolysable tannin (Smallwood and Peters, 1986; Skopec et al., 2004; Bergvall et al., 2006) and condensed tannin (Downs et al., 2003) have been reported to discourage consumption by rodents or other mammals. A definite comparison is still required to understand if the two types of tannins in seeds have different effects upon rodents' preferences.

In this study, we developed a system using artificial 'seeds'. The objective of the research was to understand how tannin concentration and the type of tannin affect rodent foraging behaviors and seed fates. The 'seeds' differed only in tannin type and concentration.

2. Materials and methods

2.1. Study site

This study was carried out in a pine forest in the Shangri-La Alpine Botanical Garden in the Hengduan Mountains, Yunnan Province, southwestern China (altitude 3456 m, 27°54′20 N, 99°38′11 E). The annual mean temperature is about 5.4 °C and annual rainfall is 625 mm, much of which occurs from May to October; the dry season lasts from November to April (Zhang et al., 2006). The forest is natural vegetation over dozens of hectares with little human disturbance. *Pinus densata* is the dominant species, accompanied by several other tree species, i.e., *Pinus armandi*, *Populus* sp., *Betula* sp., *Picea* sp., and others. The under-canopy dominant shrubs are *Quercus monimotricha* and some *Rhododendron* spp. The ground flora is poorly developed, consisting only of a few scattered herbs and mosses. The forest in the botanical garden is contiguous with the natural forest with over several hundreds of hectares, thus the rodent community in the study site was not isolated from that in the natural forest.

2.2. Tannin content in natural seeds and tannin additives

In order to know the variation of tannin contents of seeds in the forest, we collected 11 species of seeds and sent them to the Kunming Center for Food Quality Examination of Ministry of Agriculture for analysis. Seeds of all 11 species were either consumed or removed by rodents in the same forest when we placed them on ground (authors' observation). The samples were dissolved by dimethylformamide (C_3H_7NO) and the total tannin content was determined by ammonioferric citrate ($C_{12}H_{22}FeN_3O_{14}$) colorimetric method.

Tannin concentration of the 11 species ranged from 0 to 26.48%, with the mean value being 7.77 ± 2.88% (Table 1). These data helped us to design the degree of tannin concentrations in our artificial 'seeds'.

We used two types of tannins in this study: hydrolysable tannin and condensed tannin. The hydrolysable tannin used in our study was tannic acid ($C_{76}H_{52}O_{46}$, molecular mass 1701.23) which was supplied by the Reijinte Chemistry Ltd. in Tianjin of China. Condensed tannin used was a vegetable extract from barks of waxberry trees (*Myrica* sp.) (tannin concentration ≥68%, Guangshengxiang Phytochemistry Factory, Yunnan, China). Other studies have also used tannic acid as hydrolysable tannin in experiments to study animal feeding and foraging behavior (Smallwood and Peters, 1986; Bergvall et al., 2006). Downs et al. (2003) used *Acacia* leaves as condensed tannins in their study because *Acacia* leaves were high in polyphenols, primarily condensed tannins. We used *Myrica* tannins because they were standardized and commercially available.

Table 1 – Tannin contents of seeds of 11 species in the study site

Family name	Species	Tannin (%)
Cucurbitaceae	*Hemsleya pedunculosum*	0.00
Dipsacaceae	*Dipsacus chinensis*	8.32
Iridaceae	*Iris bulleyana*	26.48
Pinaceae	*Abies* sp.	25.74
Pinaceae	*Pinus armandii*	1.04
Pinaceae	*Pinus densata*	0.77
Podophyllaceae	*Sinopodophyllum hexandrum*	6.40
Ranunculaceae	*Anemone* sp.	1.95
Ranunculaceae	*Thalictrum uncatum*	7.30
Rosaceae	*Cotoneaster* sp.	0.94
Rosaceae	*Rosa omeiensis*	6.54

2.3. Artificial 'seeds' and their placement

We used clay and peanut powder to produce artificial 'seeds'. The clay was collected from the deep layer (>60 cm) of the lateritic red soil in humid tropical SW Yunnan. This clay is soft when wet and becomes hard when dry. The 'seeds' were about 15 mm in diameter, and were one half peanut powder by weight and the other half tannin and clay. By adding different amounts of tannin, we created tannin concentrations of 0.1, 0.5, 1, 5, 10, 15, and 25%, mimicking the range of tannin contents of actual seeds occurring in the study area (Table 1), and corresponding to the ranges reported in the literature (Shimada, 2001a,b; Xiao et al., 2006). Thus, we had 15 treatments including one control with 0% tannin concentration. For each treatment, we placed 108 'seeds' in six different plots (18 'seeds' per plot); in all, 1620 'seeds' were placed.

Each 'seed' was embedded with a 15 cm-long thin steel thread, and a small red plastic tag (2.5 cm in length and 0.7 cm in width) was tied to the other side of the thread. Each tag was numbered using a pencil to make each 'seed' identifiable. When rodents buried the 'seeds' in the soil, the tags were often left on the surface, making the 'seeds' easy to relocate. Most of the 'seeds' (81.3%) were relocated in this study and only 18.7% of removed seeds with no tag. Similar methods were used by some other studies (Jansen et al., 2004; Xiao et al., 2006), and the proportions of seeds relocated in their studies ranged from 39 to 55%.

In October 2006, six plots (2 m × 2 m), each >50 m apart from the closest neighboring plot, were set up. In each plot, we made nine scrapes in a 3 × 3 grid, with about 1 m between scrapes and 30 labeled 'seeds' (two seeds × 15 kinds) were released into each scrape for a total of 270 artificial 'seeds' per plot.

After the 'seeds' were released, we checked the tagged 'seeds' at each 'seed' source to record 'seeds' harvested by rodents. We searched the ground around each seed placement plot after days 1, 2, 3, 4, 6, 8, 12, and 16. We conducted a complete search within 20 m of each plot in all directions. We also conducted an extra search in a larger area in order to get as many of the seeds rechecked as possible.

The seed fates were sorted into four categories: (1) cached, i.e., buried intact in the soil and deposited intact on the surface; (2) eaten *in situ*, i.e., leaving only plastic tags and seed fragments on the ground surface of the original release plot; (3) dispersed and eaten, i.e., removed by the rodents from original release plots before being eaten; and (4) missing, i.e., not retrieved within the search area, hence with an unknown fate.

2.4. Survey of rodent communities

During the same period of seed placement, live traps were baited with fresh peanuts to determine the key rodent species that were responsible for seed disappearance. In order to minimize the effect of trapping on the rodent population in the plots where the artificial 'seeds' were released, the trapping plots were about 500 m away but in the same forest. Five transects were selected and five trap stations at intervals of 10 m were set along each of the five transects for 6 consecutive days and nights. At each trap station, two live traps were set together with their orientation reversed. Traps were checked every day at 7:30 am and 6:00 pm, and the numbers of captured rodents were recorded.

In October and November 2006, for about 15 nights, an automatically flashing camera was set in the forest about 500 m from both the live trapping sites and seed-releasing sites. The camera could take photographs of visiting animals every 10 min.

2.5. Statistical analysis

SPSS 11.5 for Windows was employed for statistical analysis. A Chi-squared test was used to test the different proportions of 'seed' fates among different kinds of 'seeds'. Linear regression models were used for examine relationships between the numbers of seeds cached and tannin concentrations. A three-way ANOVA was used to test the effects of tannin concentration and type and plots on the distance of cached 'seeds' from sites where they had been placed.

3. Results

3.1. Rodent species

We obtained 16 rodents from the night traps, but none from the day traps. Among the 16 rodents, nine were *Apodemus latronum* (56.3%), six were *A. chevrieri* (37.5%), and only one was *Eothenomys custos*.

We obtained 85 pictures with small rodents from a total of 683 pictures. There were 103 rodents in the 85 pictures; we could identify 66 of them, of which 43 were *A. latronum* (65.2%), and 23 *A. chevrieri* (34.8%). For the remaining 37, we could not identify the species clearly, but we can be sure that they were either *A. latronum* or *A. chevrieri*.

3.2. 'Seed' consumption, removal, and caching

All 1620 'seeds' were harvested after 16 days, with 1398 'seeds' (86.3%) harvested after 8 days. Of the total of 1620 'seeds', 29.4% were eaten *in situ*, and 70.6% were removed from placed plots. Among the 'seeds' removed, 31 'seeds' (2.7%) were eaten, 209 'seeds' (18.3%) were missing, and 903 'seeds' (79.0%) were cached.

There were no significant differences in the proportion of 'seeds' with hydrolysable tannin and condensed tannin cached and eaten ($\chi^2 = 0.523$, df = 1, $P = 0.469$).

The 'seeds' with different tannin concentrations showed significant differences in 'seed' fate. More 'seeds' with low tannin concentration were eaten, but cached less often than seeds with high tannin concentration, for both hydrolysable and condensed tannins (Fig. 1). Of 'seeds' with low tannin concentration (≦1%), 38.0–49.1% were cached, a proportion much lower than for 'seeds' with high tannin concentration (≧15%) (66.7–78.7%), whereas 'seeds' with low tannin concentration were eaten *in situ* (37.0–45.4%) much more frequently than 'seeds' with high tannin concentration (4.6–14.8%).

The fate of 'seeds' among different plots also showed significant differences ($\chi^2 = 500.57$, df = 5, $P < 0.001$). The

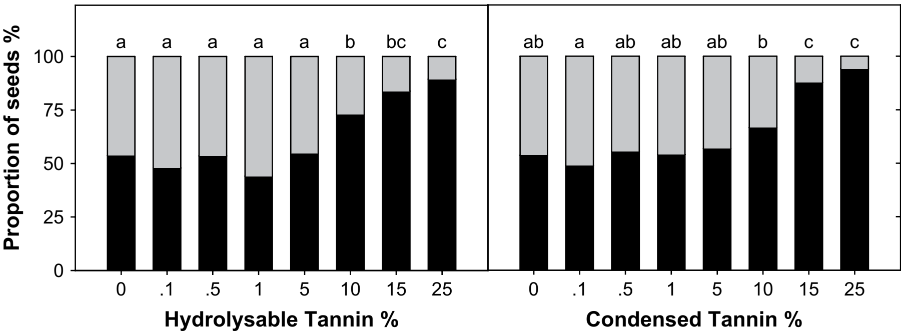

Fig. 1 – Differences of 'seed' fates among 'seeds' with different tannin concentrations (108 seeds tannin type^{-1} tannin concentration^{-1}). *Chi*-squared tests were used to test the difference of seed fates between different kinds of artificial 'seeds'. Different letters indicate significant differences among different kinds of 'seeds' ($P < 0.05$). Black bars stand for 'seeds' cached and gray bars indicate 'seeds' eaten. Only cached and eaten 'seeds' were shown, and the missing 'seeds' (12.9 ± 1.4%, mean ± SE, $n = 108$) were excluded as it showed a similar percentage across all treatments.

proportions of cached 'seeds' were very high in plots 2, 3, and 6 (81.5, 78.9 and 80.0%, respectively), but very low in plots 1, 4, and 5 (37.8, 20.4 and 35.9%, respectively), and the proportions of seeds eaten *in situ* were much greater in plots 1, 4, and 5 (54.8, 53.3, and 55.9%, respectively) than in plots 2, 3, and 6 (8.2, 1.9, and 2.6%, respectively).

A significant positive relationship between tannin concentration and the proportion of seeds cached was detected in two of the six plots and in data for the six plots combined (Fig. 2).

3.3. *Removal distance for cached 'seeds'*

Nine hundred and three seeds were cached at distances of 0–42.2 m, the mean distance being 6.3 ± 0.17 m. The mean distances of transport for hydrolysable tannin-containing 'seeds' were 6.5 ± 0.25 m ($n = 439$) and for condensed tannin-containing 'seeds' 6.3 ± 0.25 m ($n = 414$). Plots showed significant effects on the distance of 'seed' removal (Table 2). Seeds in plot 4 were cached furthest (9.50 m) and those in plot 1 were transported the smallest distance (5.22 m). Neither tannin types nor tannin concentrations had significant effects on the distance the cached seeds were transported (Table 2).

4. Discussion

Our results indicated that tannin content indeed had significant effects on seed fates (Fig. 1). There were significant positive relationships between tannin concentration and the number of cached seeds in two of the six plots and in data for the six plots combined (Fig. 2). Some other studies have suggested that rodents prefer to cache acorns with high tannin levels and consume those with low tannin levels (Shimada, 2001a; Smallwood et al., 2001; Wood, 2005; but see Xiao et al., 2006). However, as discussed in the introduction, most of these studies compared different species, and the effects of tannin concentration were often potentially confounded by other seed traits. To our knowledge, this is the first report of using artificial 'seeds' to indicate the effect of tannin concentration on the feeding preferences of rodents.

The significant positive relationship between tannin concentration and percentage of seeds cached existed at only two of the six plots. This may be because the proportion of cached seeds varied greatly among plots. The proportion of seeds cached was very high at plots 3 and 6 (78.9 and 80.0%) and very low at plot 4 (20.4%). This strong site effect may weaken, or at least obscure, the effects of tannin concentration. Site effect upon seed predation has been reported by many studies (Rey et al., 2002; Jones et al., 2003; Fleury and Galetti, 2004). Xiao et al. (2006) found that the proportion of placed seeds that were removed was higher in the primary or secondary stand than in the shrubland or the plantation, while the contrary was true for the proportion eaten. These differences were probably due to rodents' behavior, as predation risk for rodents in heavy vegetations and in open areas were different (Ostfeld et al., 1997; Manson et al., 1998; Jones et al., 2003).

Several hypotheses have been proposed in order to explain why scatter-hoarding rodents prefer to cache more high tannin seeds, as high tannin concentration itself may discourage nut consumption (Chung-MacCoubrey et al., 1997; Downs et al., 2003; Shimada and Saitoh, 2003, 2006). It has been postulated that high tannin content could be reduced in cached nuts either by abiotic environmental factors or by physiological processes in nuts (but see Dixon et al., 1997; Shimada, 2001b; Smallwood et al., 2001). Others have suggested that rodents prefer to cache nuts with high tannin content because of their lower perishability and lower probability of loss of cotyledons to insects (Wecherly et al., 1989; Smallwood et al., 2001). Studies by Steele et al. (2001) and Smallwood et al. (2001), however, indicated that germination schedule directly affects squirrel caching-preferences; they preferred to cache red oak acorns with high tannin that had a dormancy period rather than acorns from white oaks, which germinated early in the autumn. When the red oak acorns broke dormancy, they were treated like white oak acorns (Smallwood et al., 2001). A squirrel's decision whether to cache an acorn is simply based on the seed's germination schedule rather than on the tannin content of the acorn. Under this hypothesis, tannins would be merely correlated with germination schedules, but would not themselves be

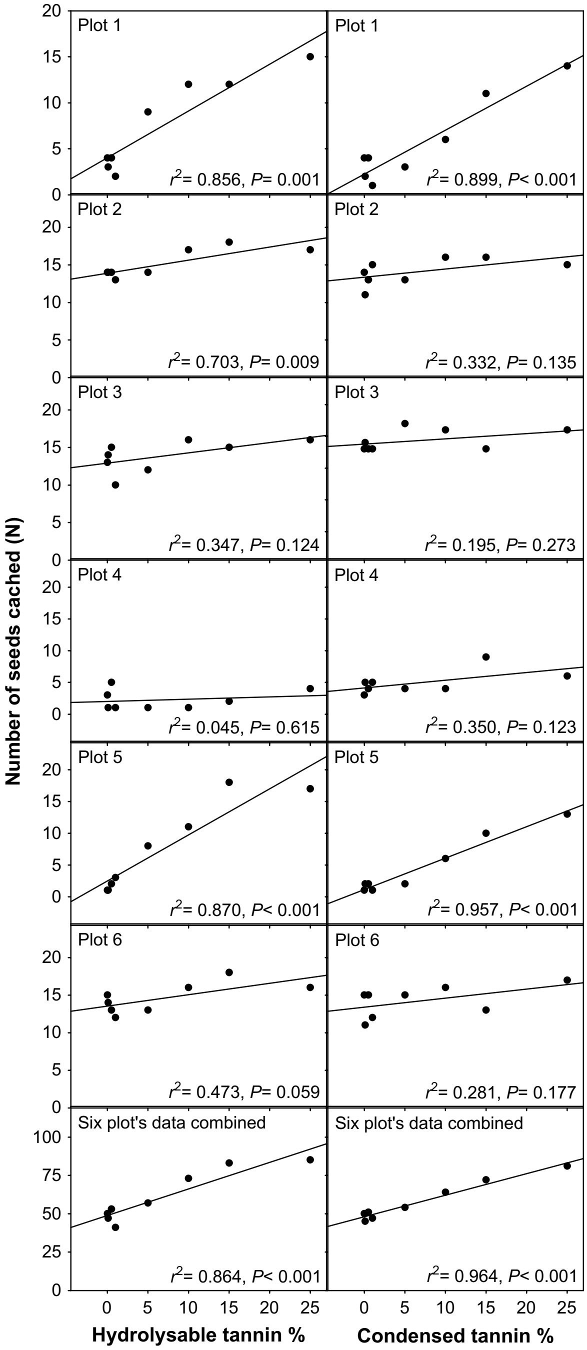

Fig. 2 – Relationships between the numbers of cached 'seeds' ($n = 903$ in total) and tannin concentration. Linear regression models in SPSS 11.5 for Windows were used to test the significance of the relationships. For each tannin concentration and tannin type, we set 18 artificial 'seeds' tannin type^{-1} tannin concentration^{-1} plot^{-1} and 108 seeds in total for each tannin concentration for both hydrolysable and condensed tannin. There are significant relationships between the numbers of cached 'seeds' and tannin concentration at plots 1 and 5 for 'seeds' with both kinds of tannins and for data from the six plots combined, but not at plots 3, 4, and 6. At plot 2, the relationship was significant for the 'seeds' with hydrolysable tannin but not for the 'seeds' with condensed tannin.

Table 2 – Three-way ANOVA summary of distance cached 'seeds' were transported ($n = 853$, not including seeds with no tannin) in relation to tannin concentration, plot, and tannin types in each experiment. The degrees of freedom (df), Means square (MS), *F*-value (*F*) and statistical significance level (*P*) of each effect and their interaction are presented

	df	MS	*F*	*P*
Tannin concentration (TC)	6	45.840	1.842	0.088
Plot (P)	5	72.131	2.898	**0.013**
Tannin type (TT)	1	12.996	0.522	0.470
TC × P	30	37.020	1.487	**0.046**
TC × TT	6	14.594	0.586	0.741
P × TT	5	9.024	0.363	0.874
TC × P × TT	30	36.392	1.462	0.054
Error	769	24.891		
Total	853			

the causal factors affecting seed fate. In our study, rodents indeed preferred to cache 'seeds' with high tannin concentration, and behavior towards the 'seeds' in our study cannot be related to germination schedules.

In contrast to its effect on the percentage of seeds cached, tannin concentration did not affect the distance that seeds were initially transported when cached by rodents (Table 2). Most studies have indicated that dispersal distances are significantly influenced by seed size (Vander Wall, 1995; Forget et al., 1998; Jansen et al., 2002, 2004; Xiao et al., 2005), which often means that rodents would behave differently depending on the different quality or amount of seeds. Tannin concentration is another indicator of seed quality, because it may affect storage ability. This study suggests that rodents may respond to different seed traits in deciding whether or not to cache seeds and how far they will transport seeds.

Different types of tannin (hydrolysable tannin *vs* condensed tannin) did not significantly affect seed fate (Table 2, Figs. 1 and 2). The tannin additives used in this study were commercial products (the only condensed tannins and hydrolysable tannins commercially available in China), which are often mixtures of different compounds and chemically not very well defined. Thus the tannin in the artificial 'seeds' was not the same as tannins with which these rodents are usually faced. Rodents' responses to different types of tannins require further investigations.

In this study, we used clay to make the artificial 'seeds'. This permitted us to construct artificial 'seeds' that were less fragile than could be constructed with peanut powder alone, facilitating relocation of the 'seeds'. However, geophagy (soil-eating) is widespread in vertebrates (Gilardi et al., 1999; Krishnamani and Mahaney, 2000; Huston et al., 2001; Brightsmith, 2004). Soil-eating may supply animals with particular nutrients (Davies and Baillie, 1988; Heymann and Hartmann, 1991) and clay may absorb and neutralize plant secondary metabolites, including tannins (Gilardi et al., 1999; Huston et al., 2001). In our study, it seems unlikely that clay positively influenced rodents' preferences, because artificial 'seeds' without peanut powder were seldom consumed or cached by rodents (authors' unpublished observations). On the other hand, we cannot exclude the possibility that tannin-clay interactions could have led to rodents to accept tannin concentrations higher than those in real seeds.

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