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Dissecting the decision making process of scatter-hoarding rodents

Bo Wang, Cheng-Xi Ye, Charles H. Cannon and Jin Chen

B. Wang, C.-X. Ye and J. Chen (cj@xtbg.org.cn), Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, CN-666303 Mengla, Yunnan, PR China. BW also at: Graduate School of Chinese Academy of Sciences, Beijing CN-100049 Beijing, PR China. – C. H. Cannon, Dept of Biological Sciences, Texas Tech Univ., Lubbock, TX 79409, USA.

Many animals scatter-hoard seeds to ensure an even supply of food throughout the year and this behavior requires similar foraging decisions. Seed-traits have been shown to affect the final foraging decision but little is known about the decision process itself. Here, we first defined four sequential steps comprising the decision process of scatter-hoarding rodents: 1) upon encountering a seed, should it be ignored or manipulated; 2) if manipulated, should it be eaten in situ or removed elsewhere; 3) upon removal, how far away should it be carried; and finally 4) whether to eat or cache the removed seed. Using experimental seeds with controlled differences in size, tannin and nutrient content, we evaluated how different traits influence each step in this decision process. We found that different traits had distinct effects on each step. Seed size affected all four steps, while nutrient and tannin content primarily affected the first and third steps. By dissecting foraging behavior in relation to experimentally controlled seed-traits, we have created an effective framework within which to understand the unique relationship between scatter-hoarding rodents that both predate and disperse plant seeds.

Any decision making process involves the selection of one course of action among several alternative options. Most decisions share common elements, like deliberation and commitment, and every decision requires a final choice (Gold and Shadlen 2007). Scatter-hoarding, i.e. the storage of food in many dispersed caches for later consumption, has been the subject of a great deal of research (Brodin 2010). Many species of animals, especially rodents and birds, scatter-hoard seeds (Vander Wall 1990). From the animal's perspective, this foraging behavior allows them to control and equalize their food supply over space and time and is an important adaptive strategy for circumventing food scarcity. Plants, on the other hand, experience both seed-predation and dispersal, with their associated costs and benefits. Furthermore, all scatter-hoarding animals face similar decisions while foraging and they should therefore share similar strategies (Sherry 1992, Sherry et al. 1992). Because successful scatter-hoarding is crucial for animal survival and long-term reproductive fitness, a more detailed understanding of the cognitive processes used by scatter hoarding animals should yield important insights into the evolution of this decision-making process (Preston and Jacobs 2005, 2009).

Both spatial and temporal aspects play important roles in the complex decision process confronting scatter-hoarding animals. In order to optimize this foraging behavior, animals must account for a series of tradeoffs, such as choosing among different species of seeds (Xiao et al. 2006), whether to consume the seed immediately or hoard it for future consumption (Preston and Jacobs 2009), and where to cache the seed (Li and Zhang 2003). This optimization strategy can be clearly outlined as a step-wise process beginning when the animal first encounters a seed until the final decision of where and when (or even if) to consume the seed (Preston and Jacobs 2009).

Most research studies have considered this complex scatter-hoarding behavior as a single process (but see Preston and Jacobs 2009), presenting only the final outcome of foraging behavior with little insight into the series of decisions themselves. Given this approach, observed seed-traits have inconsistent effects on animal foraging behavior. For example, rodents have been shown to eat low-tannin acorns in situ and hoard high-tannin acorns (Smallwood et al. 2001, Wood 2005) while the opposite results have also been found, where high-tannin seeds were eaten in situ while low-tannin seeds were dispersed (Xiao et al. 2006). To better understand how different seed-traits affect scatter-hoarding behavior, we dissect the decision making process of a common genus of Old World rodents (i.e. *Apodemus*) in Hengduan Mountains, southwestern China, using well-established artificial seed experiments (Wang and Chen 2009). We then developed three candidate models (i.e. linear model, parabolic model and segmented line model) in order to interpret the response of foraging behavior of scatter-hoarding rodents to the different seed-traits. We tested the following hypotheses: 1) the decision making process of scatter-hoarding rodents includes four distinct steps (Fig. 1): a) upon encountering a seed, should it be ignored

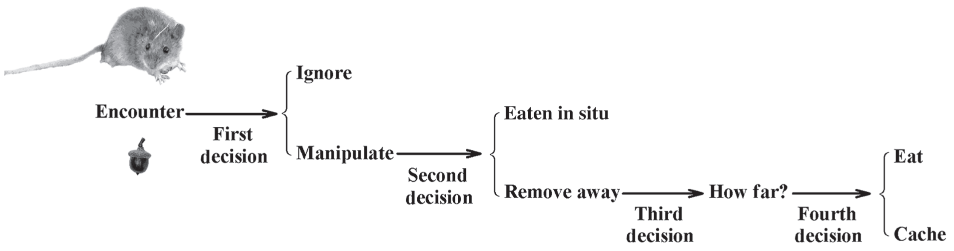

Figure 1. The four distinct steps of decision making process in scatter-hoarding rodents.

or manipulated; b) if manipulated, should it be eaten in situ or removed elsewhere; c) upon removal, how far away should it be carried; and finally d) whether to eat or cache the removed seed. 2) Different seed-traits affect the rodents' decision making process at each step differently. 3) Each single seed-trait does not have a unified or consistent effect on seed fate at all steps during the foraging process.

Methods

Model description

In this study, three candidate models were introduced to fit the relationship between the input variables X (i.e. different seed size, nutrient content and tannin content) and the decisions made by the rodents Y (rodent foraging decisions upon seeds at each of the four consecutive steps, i.e. how many seeds did the rodents manipulate, remove or cache, or how far did the rodents remove the seeds) (Fig. 2):

1) *Linear model.* Rodents' foraging decision has a linear relationship with the seed-trait. Most studies employed a simple linear regression or Pearson's correlation coefficient to determine the relationship between seed-traits and rodent foraging behavior, especially for the effects of seed size on dispersal distance by rodents (Theimer 2003, Xiao et al. 2005, Wang and Chen 2008, 2009). The model should be: $Y = bX + a + \varepsilon$, where a, b are the model parameters, and ε is the error term, which is assumed to be independent and have an identical Gaussian distribution (Fig. 2a).

2) *Parabolic model.* Scatter-hoarding rodents' foraging behavior is a series of complex decision processes, and these decisions depend on several factors. Handling time, for example, is accompanied with foraging efficiency and predation risk. Rodents usually devote different handling time given seeds with different seed-traits. For example, tannin can significantly reduce the length of time squirrels spent eating seeds (Smallwood and Peters 1986). Logically, bigger seeds usually need longer handling times. According to these possible interacting factors, the rodents' foraging decision given the seed-traits is probably not a simple linear relation, and thus a penalty term is introduced to the linear model so that the slope decreases with increasing X. So we develop the model further into: $Y = b(1 - kX)X + a + \varepsilon$, where $1 - kX$ is a penalty term and k is a parameter. This term has little effect when X is small but can significantly decrease the slope of the linear model when X is large. The parameters in the model can be found with the quadratic polynomial regression (Fig. 2b).

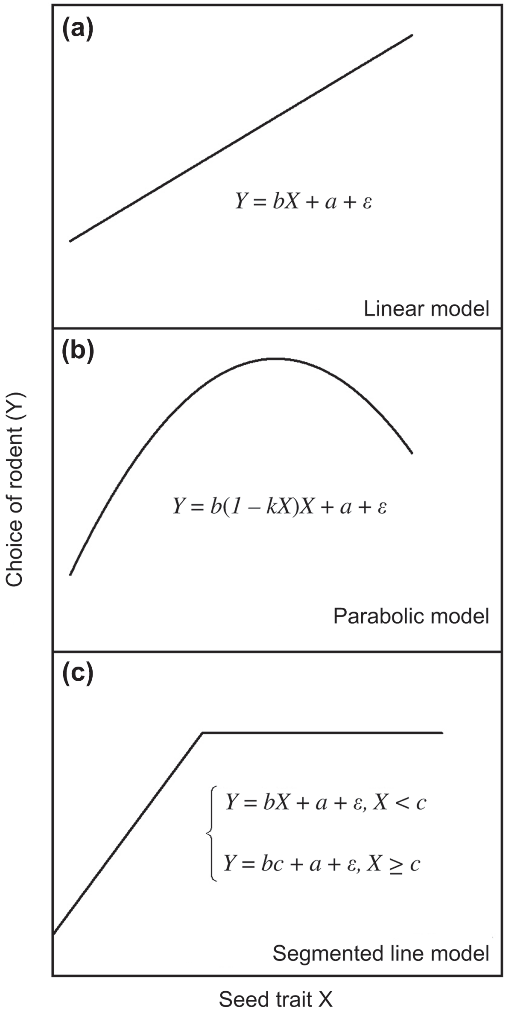

Figure 2. Descriptions of the three candidate models to explain rodent foraging preferences. X stands for different degrees of each of the three key seed-traits, and Y stands for rodent foraging decisions upon seeds at each of the four consecutive steps, i.e. how many seeds did the rodents manipulate, remove or cache, or how far did the rodents transfer the seeds. (a): linear model, rodents' foraging decision has a linear relationship with the seed-trait. (b): parabolic model, rodents' foraging decision given the seed-traits is probably not a simple linear relation, and thus a penalty term (i.e. $1 - kX$) is introduced to the linear model so that the slope decreases with increasing X. (c): segmented line model, assumes a threshold value exists for each seed-trait, being either a lower or upper limit, depending on the trait. If the seed-trait is beyond the threshold, the rodent ignores the differences of seed-trait; but within a certain range, a predictable relationship can be observed.

3) *Segmented line model*. This assumes a threshold value exists for each seed-trait, being either a lower or upper limit, depending on the trait. If the seed-trait is beyond the threshold, the rodent ignores the differences of seed-trait; but within a certain range, a predictable relationship can be observed. For example, during step one of the decision process, if a seed is big enough, the rodent would manipulate it, whether it is only slightly bigger than the threshold or if it is several times bigger than the threshold. The model should be: $\begin{cases} Y = bX + a + \varepsilon, X < c \\ Y = bc + a + \varepsilon, X \geq c \end{cases}$, where c is a constant (i.e. the threshold) (Fig. 2c). The Levenberg–Marquardt-method was used to find the estimates of the parameters for the segmented line model (Smith et al. 2010).

Empirical data collection

The experimental data analyzed here was collected in 2007 at the Shangri-La Alpine Botanical Garden (27°54′N, 99°38′E, altitude 3456 m a.s.l.), Yunnan province, southwestern China, in natural forest where *Pinus densata* is the dominant tree species and *Apodemus latronum* and *Apodemus chevrieri*, both rodents, were the two most abundant seed predators and dispersers in the forest (Wang and Chen 2009). Both rodent species have similar body sizes (T-test, $p > 0.05$), 28.0 ± 5.9 g (mean ± SD, $n = 24$) for *A. latronum* and 32.5 ± 8.5 g ($n = 16$) for *A. chevrieri*, and they showed similar foraging behavior given the experimental seeds (Wang and Chen 2011). We did not consider the effects of seed consumption and dispersal by birds, ants or other animals in this study, because none were consumed or removed by these animals in this study.

Our experimental design used three univariate series of experimental seeds made from clay, peanut powder (i.e. nutrient) and tannin that tested the response in scatter-hoarding rodent foraging behavior to three important seed-traits. Our previous studies found that rodents in the field not only eaten, but also carried away and cached the artificial seeds, just like the they did to the natural seeds (Wang and Chen 2008, 2009, 2011). Unlike real seeds, experimental seeds have no hull, which is a very important variable in seed choice and handling behavior of rodents. However, this approach could still provide some insights into the relationship between rodents and existing plant species and the specific seed-traits themselves. In this study, clay was used to make the experimental seeds for two reasons: 1) it helped with maintaining the other traits constant while we changed the content level of one target trait because the clay contained neither tannin nor nutrient; 2) it allowed us to construct robust experimental seeds because of its viscosity. The clay itself did not positively influence rodent foraging preferences, because experimental seeds made from pure clay were seldom consumed or cached by rodents (Wang et al. unpubl.). In order to determine the variation in seed size, nutrient and tannin contents of seeds, we collected 11 common species of seeds in the forest for analysis. The mean caloric content of the 11 species was 10.29 ± 1.30 kJ g^{-1} (mean ± SE), with a range of 2.37–18.80 kJ g^{-1}. Tannin contents had a range of 0–26.48%, with a mean of 7.77 ± 2.88%. These data were used as a guideline for the nutrient and tannin contents in our experimental seeds. The mean seed length was 0.8 ± 0.1 cm, with a narrow range of 0.4–1.4 cm. Thus, in order to get a much clearer pattern about the rodent foraging decisions upon seed size, we expanded the variation of our experimental seed size, from 0.2 to 4.0 cm.

The three univariate series of experimental seeds are: 1) Size – ten values, including 0.2, 0.4, 0.6, 0.9, 1.2, 1.5, 2.0, 2.5, 3.0 and 4.0 cm in diameter (a total of $108 \times 10 = 1080$ seeds), and each seed consisting of 50% peanut powder and 50% clay; (2) Nutrient content – eight values, with the following percentage of peanut powder: 0, 10, 20, 30, 40, 50, 60 and 70 (totaling $108 \times 8 = 864$ seeds), and each seed with the same size (15 mm in diameter); the seeds with 0% nutrient content were made of 100% clay, but given the odor of peanut powder, because the water used in preparing these seeds was first soaked with peanut powder, and that soaking on peanut powder would lead to negligible increase in nutrient contents of seeds; (3) Tannin – seven values of percent tannin content, including 0.1, 0.5, 1, 5, 10, 15 and 25, and each seed with the same size (15 mm in diameter), consisting of 50% peanut powder, and the other 50% being clay and tannin. A different series was created for hydrolyzable and condensed tannins separately, with one control containing no tannin, giving a total of $108 \times 15 = 1620$ seeds. As no difference in the effects of the two types of tannin on rodent foraging behavior existed (Wang and Chen 2008, 2009), these two tannin series were combined into a single treatment in subsequent analysis. A 15 cm thin steel thread with a small red plastic tag was connected to each experimental seed, using modified methods from some previous studies (Forget 1990, Forget and Milleron 1991, Xiao et al. 2006). Each tag was numbered for seed identification. When rodents buried the seeds in the soil, the tags were usually left on the surface, making the seeds easy to relocate.

Six plots (2×2 m) > 50 m apart from each other were set up in the forest to conduct the three univariate-trait experiments one by one. At each plot, we located nine subplots in a 3×3 grids, with about 1 m between subplots. Each circular subplot was about 15 cm in diameter, and the seeds were placed along the circle with the tags located outwards. Two seeds of each trait variant (size or nutrient or tannin content, only one seed-trait per plot each time) were placed in each subplot. Each trait variant was represented by 108 seeds spread evenly over the six plots (two seeds × nine subplots × six plots). After the seeds were placed at each plot, we checked and recorded the fate of the seeds encountered by the rodents after 1, 2, 3, 4, 6, 8, 12, 16, 20, 28 and 36 days. We conducted a completed search within 20 m of each plot in all directions to relocate the removed seeds. We also conducted an extra search in a larger area in order to relocate as many of the seeds as possible (see Wang and Chen 2009 for full details of our experimental design).

The data we collected were defined as follows: 1) percentage of seeds manipulated by rodents, including seeds both removed and eaten in situ (i.e. leaving only plastic tags and seed fragments in the original plot); 2) seeds removed, including all possible removal fates: cached (buried intact in the soil or deposited intact on the soil surface), eaten after being transported (removed by the rodents from the original release plots before being eaten) and missing (seeds that were not found within the search area, hence with an unknown fate); 3) removal distance, the distance between the seed we found and its original position; and 4) seeds cached after removal. Since almost all experimental seeds were manipulated by the end of experiment, manipulating preference of rodents on the first day of the experiment was used to evaluate the first step in the foraging decision process, i.e. whether to manipulate the seed or not.

Data analysis

Three model selection methods, maximizing fit (R^2), Akaike's information criterion (AIC) and Schwarz's Bayesian information criterion (BIC), were used to evaluate the candidate models (Johnson and Omland 2004). For $R^2 = 1 - \frac{SS_{err}}{SS_{tot}}$, where SS_{tot} is the total sum of squares, and SS_{err} is the sum of squares of residuals. The p-value is calculated according to the F-statistics. The AIC and BIC are calculated in an equivalent form: $AIC = 2p + n\ln RSS$ and $BIC = p\ln n + n\ln RSS$, where p is the number of free parameters to be estimated, n is the sample size, and RSS is residual sum of squares for a linear model. Optimal models should be the ones with lowest AIC and BIC value, and statistically significant R^2 value (i.e. p-value < 0.05). ΔAIC (or ΔBIC) shows the change in AIC (or BIC) compared to the best model. Models within 2 ΔAIC (or ΔBIC) units have equivalent empirical support (Hautier et al. 2010). Model selection processes were conducted in MATLAB 2010.

Results

The three different seed-traits (size, nutrient content, and tannin content) indeed affected each of the four steps of scatter-hoarding foraging behavior differently (Fig. 3). Seed size significantly affected all steps: the first step (when a seed is encountered, is it manipulated or ignored), the second (eaten seeds in situ or removed them away), third (how far should the seed be removed) and forth steps (eaten or cached the removed seed), while both nutrient and tannin content mainly affected the first and third steps.

Additionally, the rodent foraging response to each seed-trait varied at each step in the decision process, typically following different regression models. The effect of seed size on the first and fourth steps followed the parabolic model, explaining 83.6% and 78.5% variation, respectively (Fig. 3a, d). The optimal seed size, in terms of percentage of seeds manipulated and seeds cached, was slightly less than 2.0 cm. The segmented line model best described rodent response at the second and third steps but the seed size threshold differed substantially: seeds with the diameter > 0.9 cm were not removed according to a linearly increasing proportion, all removed at a similar high rate (~80%) (Fig. 3b), while seeds with the diameter > 3.0 cm were not removed according to a linearly increasing distance, all up to ~15 m (Fig. 3c).

Seed nutrient content primarily affected the percentage of seeds manipulated and the distance of removal (Fig. 3e–h). A linear relationship existed between manipulating rate and percent nutrient content up to 50%, at which point 100% of the seeds were manipulated on the first day. The first step followed the segmented line model which explained nearly 98% variation. Rodents manipulated more high-nutrient seeds, however, when the nutrient of the seeds are beyond a threshold ($\approx 52.8\%$ of peanut powder), rodents perform no bias among seeds thus manipulated all of them (Fig. 3e). Removal distance (step 3) generally increased with nutrient content until seeds contained 50% peanut powder, above which removal distance declined slightly, fitting the parabolic model best, explaining 89.3% of the variation. The model showed that maximum distance (≈ 15.0 m) seemed to have an optimum at 62.7% of peanut powder. While the parabolic model fit the relationship between seed nutrient content and proportion of cached seeds (Fig. 3h), the overall variation was small and no significance difference existed (ANOVA-test, $p = 0.763$).

Tannin's effects mainly existed in the first step, following parabolic model ($R^2 = 0.975$, $p < 0.001$). The function showed that high tannin content seeds would be manipulated much less than low tannin content ones (Fig. 3i). Tannin content could also affect the third step, low tannin seeds would be removed further than high tannin ones. Both parabolic model and linear model could fit the third step, explaining 90.5% and 85.3% variation, respectively (Fig. 3k). Interestingly, tannin content affects the fourth step in a contrary way; high tannin content seeds would be cached much more than low tannin content ones. The parabolic model could fit that step, with the maximum cache proportion seemed to have an optimum at 14.7% tannin content, indicating the positive relationship only occurred within certain tannin content (~15%) (Fig. 3l).

Discussion

Our results have clearly demonstrated that variation in seed-traits do not have a unified or consistent effect on seed fate but instead is best described by a step-wise model for the foraging behavior of scatter-hoarding rodents. Instead, the behavioral response of the rodents varied according to each step in the decision making process, indicating that the animals evaluate the cost and benefits associated given different seed-traits at each discrete step. Therefore, dissecting the decision process as we do here can provide an effective perspective on animals' scatter-hoarding behavior. For the plant, this perspective also reveals the complexity of the optimal suite of seed traits for effective dispersal as a single seed-trait can cause different responses at different steps in the decision process. For example, high levels of tannin reduce the probability of being removed and the distance removed, while ultimately, they increase the likelihood, if removed, that the seed will be cached. We feel that this perspective will yield important insights for a better understanding of the relationship between plants and the scatter-hoarding animals.

Not only did rodent foraging behavior respond differently to the experimentally controlled seed-traits in our study (size, nutrient and tannin content) but these responses often fit different behavioral models. All three seed-traits

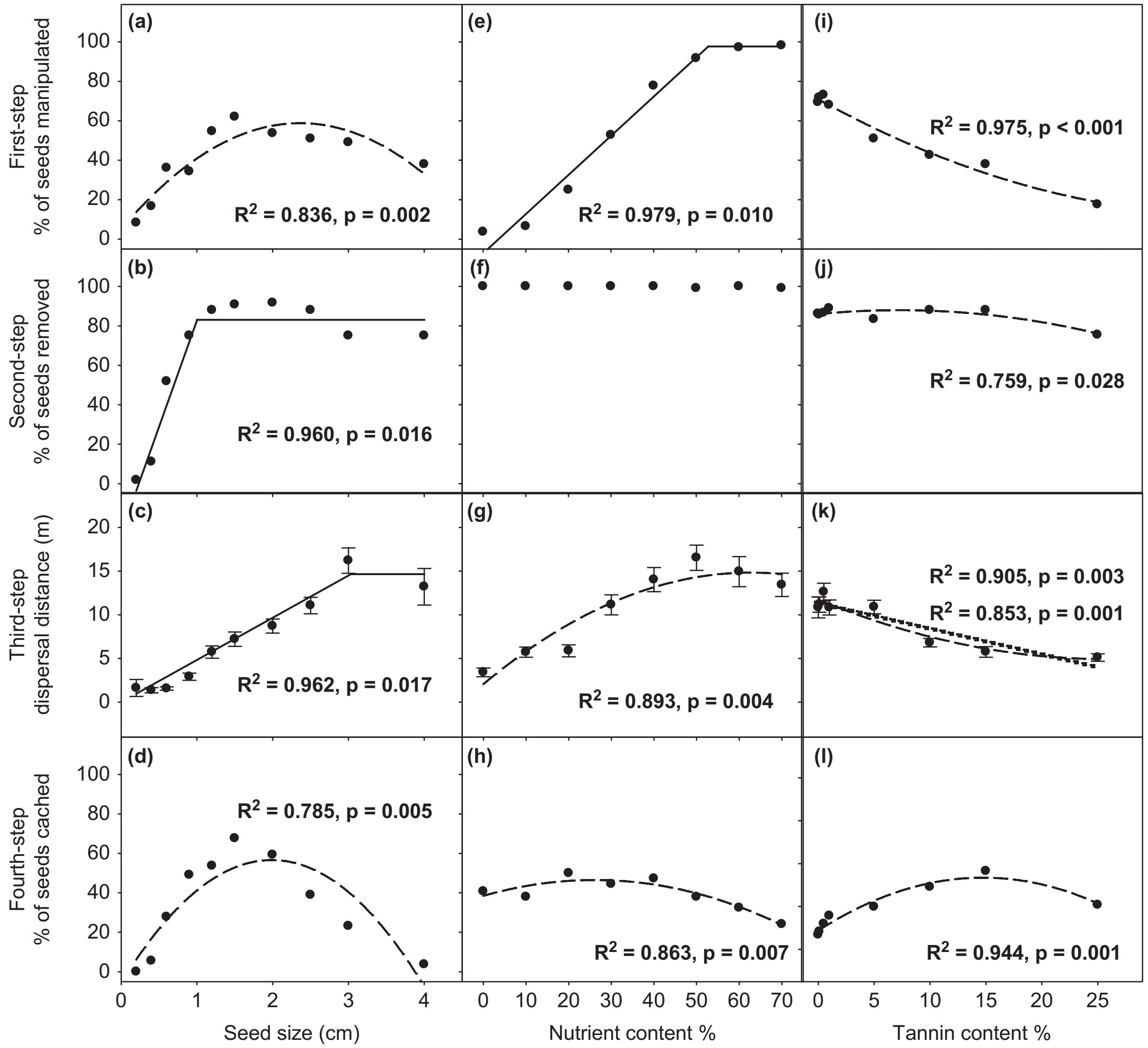

Figure 3. Model selection results of seed-trait effects upon each step of rodent foraging process. First steps of choice, seeds manipulated in the first day; second choice, seeds removed; third choice, distance carried by the rodents; forth choice, seeds cached. Only the models with less than 2 ΔAIC (or ΔBIC) units and significant R^2 values were displayed (Supplementary material Appendix 1, Table A1–A3). ΔAIC (or ΔBIC) showed the change in *AIC* (or *BIC*) value compared to the best model. Models within 2 ΔAIC (or ΔBIC) units have equivalent empirical support. Dotted, dash and solid lines stand for linear model, parabolic model and segmented model, respectively. Error-bars used in (c), (g) and (k) are ± SE (more details about the models can be found in the text). (a–d): effects of seed size upon each of the four steps of rodent foraging process; (e–h): effects of nutrient content of seed upon each step of rodent foraging process; (i–l): effects of tannin content of seed upon each step of rodent foraging process.

significantly affected the rodents' choice at the first step (Fig. 3), indicating a seed, once encountered, had to meet several quality control criteria before it was manipulated. The decision to manipulate the seed is obviously the most important from both the rodent and plant perspectives and intensively impacts subsequent foraging steps and the success of food storage and seed cache (and thus dispersal). At this initial encounter, the rodent assesses the seed comprehensively and to maximize the chances of the rodent manipulating the seed, the plant must provide the appropriate mixture of seed-traits. During this assessment, intermediate sized seeds have the highest chance of being manipulated. High nutrient content rapidly increases manipulating rate and high tannin content decreases manipulating rate gradually. Several studies have discussed how seed value affects the rodent decision to manipulate a seed or not. For examples, some studies found significant relationships between seed manipulate and seed size (Blate et al. 1998) while others did not (Kollmann et al. 1998, Moles and Drake 1999). Moles et al. (2003) found a weak negative correlation between seed mass and the percentage of seeds manipulated after 24 h of exposure to post-dispersal seed predators at two of three field sites in Australia, but no significant relationship across 280 species from the global literature. These inconsistent results may come from the different range of seed size in their experiments, as intermediate sized seeds have the highest chance of being manipulated (Fig. 3a).

The vast majority of seeds are removed rather than eaten in situ, except for the smallest seeds (< 0.9 cm) (Fig. 3b, f, j), indicating that the second step (remove or not) is a relatively trivial one and most seeds are removed, once manipulated. Some other studies have also shown that seeds with larger size or higher energy content are more likely to be removed rather than eaten in situ by scatter-hoarding rodents (Vander Wall 1995, 2003, Forget et al. 1998, Jansen et al. 2004, Xiao et al. 2006, Wang and Chen 2009). Effects of seed size upon seed removal followed the segmented line model in our study, explaining 96.0% of the total variation. It is logical that handling larger seeds may take more time and a tradeoff between handling time and avoiding foraging risk should exist. Thus, the seeds should be carried to a safer place, whether to be eaten or cached, if they are bigger than a threshold. Nutrient and tannin content showed little effect upon this step, and this may because of the size of these nutrient and tannin content seeds, all being 1.5 cm. As long as seeds were greater than ≈ 1.1 cm in diameter, rodents treated them all the same way, i.e. removed them away (Fig. 3b). Experimental seeds used in both nutrient and tannin experiments were the same size, about 1.5 cm in diameter. So, it makes sense that rodents removed almost all seeds, regardless of nutrient/tannin content.

The third decision (how far to remove) involved a similar response to seed-traits as the decision about whether to manipulate the seed. While both seed size and nutrient content had a generally positive relationship with removal distance, greater size led to linear increases in removal distance until the largest seed size tested; while a positive parabolic model best fit the data for nutrient content, i.e. removal distance generally increased with nutrient content until seeds contained 50% peanut powder, above which removal distance declined slightly. The response to tannin content at this step was almost identical to the first step, with a slight parabolic decline in removal distance with increasing tannin content. Most studies focus on the effects of seed size on removal distance. For example, a positive correlation between seed size and dispersal distance when seeds are small (less than 6.5 g) has been observed (Xiao et al. 2005, Moore et al. 2007, Takahashi et al. 2007). Jansen et al. (2002) found that the maximum distance of cached seeds of a large-seeded tree species (*Carapa procera*, mean = 21 g) by the acouchis reached an optimum mass of 29 g, above which dispersal distance decreased. In another large-seeded species, *Beilschmiedia bancroftii* (mean = 51.2 g), Theimer (2003) found no relationship between seed size and dispersal distance by rodents. Some big seeds might have exceeded the threshold seed size, and manipulation became increasingly difficult and more energy was required (Fig. 3c), which could have been revealed in a step-wise analysis of the decision process.

The final decision about whether to cache the seed or not is where the response differed substantially from the other steps. Seed size had a strongly parabolic effect, with the largest seeds almost all being eaten and not cached, although the seeds with the greatest chance of being cached were comparable to the seeds with the greatest chance of being manipulated. Generally, large seeds are more likely to be removed and then cached rather than eaten in situ by scatter-hoarding rodents (Forget et al. 1998, Vander Wall 2003, Jansen et al. 2004), for several reasons: longer storage time, a smaller number of cache sites that rodents must remember (Jansen et al. 2002). In our study forest, the largest sized natural seeds are those intermediate sizes in the artificial seed system, for examples, *Pinus armandii* and *Quercus monimotricha*, which were mainly dispersed by rodents (Wang et al. 2012, unpubl.). Our results demonstrated the medium sized seeds were the most likely to be cached, potentially due to the small body size of the rodent species (i.e. *Apodemus*, only several tens of grams) in our study site (Wang and Chen 2009, 2011). There should be a threshold of seed size beyond which handling become increasingly difficult and expensive for these small rodents. Munoz and Bonal (2008) also indicated the importance of considering both seed and rodent body sizes in these types of studies. Large caches or even small caches of large seeds are more likely to be lost due to pilferage (Janzen 1971, Clarkson et al. 1986, Zhang and Zhang 2007). Otherwise, caching is a behavior which cost lots of energy, including excavating, disguising, remembering, checking, protecting and manipulating. Logically, the energy expenditure of these behaviors should be positively related to seed size and the ultimate decision to cache or not should be a tradeoff between the costs and benefits of caching, especially for smaller rodents, like those in our study site. Alternatively, the fate of larger seeds was more likely to remain unknown ($R^2 = 0.929$, $p < 0.001$), indicating the observed proportion of the largest seeds cached in our study is an underestimate of the actual proportion cached. Similarly, seeds with nutrient content greater than 20–30% were eaten more frequently than cached. A major difference at this step can also be observed in the effect of increasing tannin content, which generally increased the chances that the seed would be cached instead of eaten, except at the greatest tannin concentrations. Tannin can prevent seeds from being eaten by insects (Weckerly et al. 1989, Smallwood et al. 2001) and tannin content is usually correlated with delayed germination time (Smallwood et al. 2001, Steele et al. 2001). Therefore, seeds with high tannin concentrations can be stored for longer periods of time without nutrient loss and rodents can benefit more from their caches. Some other studies also suggested that rodents prefer to cache acorns with a high tannin level (Shimada 2001, Smallwood et al. 2001, Wood 2005, Xiao et al. 2008; but see Xiao et al. 2006, Wang and Chen 2009). Although most of the current studies mentioned above always focused on the tannin effects upon rodents' foraging decision to eat versus hoard a seed, several other secondary chemicals were also found to influence this decision. For example, quinolizidine alkaloids were found to reduce seed predation but not caching by agoutis (Guimaraes et al. 2003). Cyanogenic glucosides, terpenes, oxyacanthine, chelidonic acid were also found to be a defense in seed predation by rodents (Sherbrooke 1976, Kollmann et al. 1998), however, the effect of these chemicals on the caching decision is unknown.

The patterns indicate that while the seed-traits generally drive rodent response towards similar results during the first three steps, with increasing size and nutrient content but decreasing tannin content generally improves the probability of being manipulated, removed, and removed greater distances, the seed-traits that improve the chances of a favorable outcome for the plant, that the seed be cached and essentially planted by the rodent, are substantially different: small to intermediate seed sizes and nutrient contents and intermediate to high levels of tannin. These differences illustrate the tension in the relationship between the rodent and plant and the power of dissecting this interaction into discrete steps, as the plant must balance the advantage of seed-traits at several early interactions against conflicting advantages at the last and critical step.

A number of papers have also shown fate diagrams of seeds that consider numerous steps from seed production to germination (Vander Wall 2002, Jansen et al. 2004, Xiao et al. 2005). For examples, Jansen et al. (2004) tracked seeds from their original releasing site, primary cache, secondary cache, and so on, until germination. However, most of these studies usually consider the rodent foraging decision between encounter to cache as a single process. Preston and Jacobs (2009) divided the caching decision of fox squirrels by into two consequent processes: assessing seed quality and assessing seed weight to decide whether to eat or cache the seeds. In our study, scatter-hoarding rodents' foraging process has been divided into four consecutive steps, resolving some of the potentially conflicting results obtained in previous studies. For examples, some studies have shown that rodents prefer to cache seeds with high tannin content but consume in situ those with low tannin content (Smallwood et al. 2001, Wood 2005, Wang and Chen 2008); while others not (Xiao et al. 2006, Wang and Chen 2009). Our results demonstrate that tannin content affects seed manipulating and caching rates in opposite directions, particularly at the final step in the interaction, potentially explaining the inconsistent results about rodents' choice. Many studies have shown that seed abundance, rodent population size and other environment factors had significant effects upon rodents foraging behavior (Vander Wall 2002, Fleury and Galetti 2004, Jansen et al. 2004). For example, Jansen et al. (2004) found that portions of seeds eaten and cached by rodents were different between seed-rich and poor years. So, for the year that high rate of seed suffering in situ consumption will possibly yield tannin negatively correlated to final seed survive; while for the year that high rate of seed transported, seed tannin might be positively correlate to the final survival rate of seeds. By giving careful attention to the detailed interaction between rodent and plant, mediated through seed-traits, at each step in the decision process, we feel that further insight and understanding can be gained about this fascinating obligate plant–animal interaction.

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Supplementary material (available online as Appendix O20823 at <www.oikosoffice.lu.se/appendix>). Appendix 1.