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Effects of seed traits on the cache size of a scatter-hoarding rodent, Leopoldamys edwardsi

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Abstract

Seed traits can influence post-dispersal seed fate and seedling establishment by manipulating the size of caches made by hoarding animals. However, few studies have explored how seed traits affect cache size and subsequent seed fate mediated by hoarding rodents. In this study, we investigated the effects of seed traits on hoarding behavior of *Leopoldamys edwardsi*using seeds of *Quercus variabilis*, *Castanea henryi*, *Camellia oleifera*, *Lithocarpus harlandii,* and *Choerospondias axillaris*under enclosures in Dujiangyan City, southwest China, in an attempt to elucidate the relationship between seed traits and cache size. Our results showed that there were significant differences in the scatter-hoarded preference among *C. axillaris*, *C. henryi*, *C. oleifera*, *Q. variabilis* and *L. harlandii* by *L. edwardsi.* There was a significant difference in the cache size between five seed species by *L. edwardsi*. More importantly, we found that there was a significant positive correlation between cache size and the proportion of intact after removal or crude fat, but a significant negativecorrelation between cache size and seed mass or crude starch. Our study has revealed that seed traits are a key factor in regulating the hoarding behavior of rodents, which includes the size of their caches. This behavior, in turn, has a significant impact on the fate of the seeds and the growth of seedlings that emerge from the caches.

Significance statement

At present, a large number of studies focus on a certain trait of a single seed or the effect of a certain seed trait of various seeds on the hoarding behavior of rodents, but how seed traits affect cache size and subsequent seed fate mediated by hoarding rodents remains unknown. This study systematically illustrates how rodents build storage sites and determine the seed fates according to seed traits. Establishing food storage sites based on different seed traits involves a trade-off between the recovery rate and the pilfering rate of food-hoarding sites, which may be an adaptive storage strategy formed in the long-term evolution process.

Introduction

The cache size refers to the number of seeds buried in each cache when an animal stores seeds. During seed storage, rodents tend to alter their hoarding tactics based on seed traits and the prevailing environmental conditions (Geluso 2005). The size of a rodent's cache is considered to be an important adaptive strategy for preventing food loss (Zhang et al. 2016). Previous studies have demonstrated that various seed traits, including seed mass, nutrient content, seed coat thickness, and odor intensity, can significantly influence the behavior of rodents when it comes to consumption and pilfering (Vander Wall. 2010; Yi et al. 2015; Zhang et al. 2016; Lichti et al. 2017; Chen et al. 2022; Xiao et al. 2022). The thickness of the seed coat can also lead rodents to defer consumption or leave seeds in the ground (Yang et al. 2023). In previous paper, it was found that the average and maximum scatter-hoarding distances of large seeds were significantly greater than those of small seeds (Vander Wall 2003; Xiao et al. 2006; Lai et al. 2014; Zhang et al. 2016). Therefore, it is crucial to comprehend the significance of seed traits in facilitating successful seed dispersal and the impact of rodents in selecting for these traits, and this

understanding is vital for future research on seed dispersal mechanisms (Wang and Chen 2009; Wang et al. 2014; Yi and Wang 2015; Lang and Wang 2016; Zhang et al. 2021).

Seed traits appear to be the subject of natural selection, as plant seeds compete by scatter-hoarders, influence whether seeds are stored and how far they are transported, and attempt to avoid high levels of seed pilfering risk by competitors (Vander Wall 2010). Seeds that have low nutritional value can be stored for a longer period compared to those with high nutritional value (Barga and Vander Wall 2013), and large seeds with high nutritional value will be stored in more spatial memory by rodents during cache retrieval (Yi et al. 2021). The high-nutrition hypothesis holds that rodents consumed more seeds with low fiber content and cached high-nutrition seeds (high fat and calorific value) (Lewis 1982; Zhang et al. 2015). Moreover, A large amount of evidence shows that rodents preferentially select large seeds with high nutritional value and high secondary metabolite content, and consume small seeds with low nutritional value and low chemical defense (Jansen et al. 2004; Chang et al. 2009; Vander Wall 2010). Studies have also shown that rodents put more spatial memory in seeds with weak odors and tend to scatter-hoard seeds with weak odors (Yi et al. 2016; Li et al. 2018)

As such, understanding the relationship between cache size and scatter-hoarding behavior is crucial for predicting the impact of rodents on seed dispersal and plant regeneration in ecosystems. It is not only related to the recovery rate of scatter-hoarded seeds, but also determines the pilfering risk (Vander Wall et al. 2009; Xiao et al. 2015; Vander Wall et al. 2018). Scatter-hoarded rodents adjust the cache size based on the seed traits of the seeds they are storing. Furthermore, the cache size of rodents indirectly determines the establishment, competition, survival, and regeneration of seedlings (Jansen et al. 2004; Vander Wall et al. 2009; Xiao et al. 2015; Zhang et al. 2016). Thus, the study of the effects of seed traits on the cache size of rodents not only can provide an in-depth understanding of the scatter-hoarding behavior of rodents but also can reveal the co-evolutionary relationship between rodents and plant seeds (Xiao and Zhang 2004; Yang et al. 2018, 2022), and then play a key role in maintaining local seed dispersal and plant regeneration (Xiao et al. 2005, 2006; Cheng et al. 2005a).

Leopoldamys edwardsi, one of the dominant scatter hoarders in the subtropical evergreen broad-leaved forest in the Dujiangyan region, consumes and caches a variety of plant seeds, such as *Quercus variabilis*, *Q. Serrata*, *Lithocarpus harlandii*, and *Camellia oleifera* (Xiao and Zhang, 2004; Yang et al., 2018, 2022), and they play an important role in maintaining local seed dispersal and plant regeneration (Xiao et al. 2006, 2008; Cheng et al., 2005). At present, a large number of studies focus on a certain trait of a single seed (Cheng et al. 2005b; Chang et al. 2008) or the effect of a certain seed trait of various seeds on the hoarding behavior of *L. edwardsi* (Xiao et al. 2008), but there is no systematic study on the relationship between cache size and seed traits of sympatric seed species. To reveal the relationship between cache size and seed traits, we carried out seed hoarding experiments of *L. edwardsi* under enclosure conditions. The seeds used in the experiments were from *Castanea henryi*, *Q. varialilis*, *L. harlandii*, *C. oleifera*, and *Choerospondias axillaris*, which possess varying seed traits.

Methods

Study Site

This experiment was carried out from September to December 2018 at the Banruosi Experimental Forest in Dujiangyan city, Sichuan Province (altitude 700–1000 m). Dujiangyan region (30°45 '~ 31°22 'N, 107°25' ~ 103°47 'E) belongs to the Sichuan Basin and is the transition zone from the Qinghai-Tibet Plateau to the Chengdu Plain. It is in a special location where various geographical factors meet and transition. The annual average temperature is approximately 15°C rainfall is abundant, and annual precipitation is 1200 ~ 1800 mm. The geographic location belongs to the middle subtropical region with more fog, less sunshine (annual sunshine duration 800 ~ 1000 h), and high humidity (annual average relative humidity more than 80%). The major vegetation type is a natural secondary forest dominated by *Q. variabilis*, *Q. serrata*, *L. hancei*, *Cyclobalanopsis glauca*, *C. axillaris*, and *C. oleifera* (Yang et al. 2018, 2022). *Castanea henryi* is the dominant tree species in a nearby forest, Qingcheng Mt. (One national forest park), ca. 20 km from the Banruosi Experimental Forest (Xiao et al. 2008).

Study animals

In August 2018, live steel traps were used to capture rodents in the Dujiangyan field area. Using peanuts as bait, 33 adult *L. edwardsi* (13 20) were captured. Previous studies have shown that *L. edwardsi* is a dominant scatter-hoarding species in this study site (Chang et al. 2009; Yi et al. 2021). All *L. edwardsi* were kept in separate cages in the laboratory after the gender and weight were recorded. The natural temperature was maintained in the lab and adequate food, water, and bedding were provided in the cages. Healthy adult rodents were selected for the hoarding experiment. Before the experiment, all rodents were provided with the same amount of food.

Enclosures

Hoarding experiments were carried out in five identical 10 m × 10 m indoor enclosures. The floor of the enclosure is paved with red bricks to create 64 shallow pits, which are filled with fine sand, allowing *L. edwardsi* to scatter-hoard seeds (Yi et al. 2021; Wang and Yi 2022). A nest box (40 cm × 40 cm × 40 cm) was placed in the two opposite corners of each enclosure and an appropriate amount of wood chips was placed to keep the rodents warm. Two drinking pans were prepared next to the nest box to provide *L. edwardsi* with plenty of water during the experiment. During the experiment, a certain number of seeds were placed in the seed station for *L. edwardsi* to store or consume.

Seed species and seed labelling

In autumn 2018, mature seeds of *C. axillaris*, *L. harlandii*, *C. oleifera*, *Q. variabilis*, and *C. henryi* were collected under the tree and healthy seeds with similar size were selected for the enclosure experiments. Since the origin of the seeds is the same, the trait parameters of the seeds including seed mass, crude starch, crude fat, crude protein, crude fiber, tannin, and caloric value in this study refer to previous studies

in this region (Xiao et al. 2008; Yang et al. 2020). We inserted a passive integrated transponder (PIT) tag with a unique code (model: RBC-1.4*8B-B-J; 1.4 mm × 8 mm, 0.03 g) into a small hole (1.5 mm in diameter) drilled on each of seed and ensure that the PIT tag will not fall off during seed handling by rodents. This marking method is different from the plastic plate marking method commonly used in previous studies and has little influence on the experiment (Gu et al. 2021).

Hoarding experiments

Prior to the formal experiment, *L. edwardsi* was introduced into the experimental enclosures for adaptation, during which adequate food and drinking water were provided. One day after acclimation, each individual of *L. edwardsi* was provided with the tagged seeds of one given tree species in the center of each enclosure for scatter-hoarding and consumption. The number of seeds provided to *L. edwardsi* was 40 for *C. axillaris* (seed mass: 2.235 ± 0.351; mean ± SD), 40 for *L. harlandii* (3.487 ± 0.795), 50 for *C. oleifera* (1.499 ± 0.348), 40 for *Q. variabilis* (5.145 ± 0.940) and 40 for *C. henryi* (6.183 ± 0.887). Ten hours later, *L. edwardsi* was removed from the enclosure, and pits were scanned individually with a hand-held reader (Model RBC-S03, Anhui Raybaca IoT Technology Co., Ltd., China) to see how many tagged seeds were cached by *L. edwardsi* was recorded. To avoid signal interference caused by multiple PIT labels cached in the same pit, we scanned several times for each pit to ensure that all seeds that had been cached were detected. Cache size refers to the number of seeds that were cached in each pit by *L. edwardsi*. Seed fates were divided into 1) intact in situ (IIS) : seeds remained at the seed station; 2) eating in situ (EIS): seeds were eaten at the seed station; 3) intact after removal (IAR): seeds were removed but not consumed; 4) eaten after removal (EAR): seeds were removed and consumed; 5) Larder-hoarded (LH): seeds hoarded in the nest boxes; 6) Scatter-hoarded (SH): seeds were hoarded in the shallow pits. After that, all residual seeds and rodent feces were cleaned for another batch of hoarding experiment.

In this study, 12 *L. edwardsi* (6 , 6) were randomly selected for hoarding experiments of *Q. variabilis*, 17 *L. edwardsi* (7 , 10) for *C. henryi*, 25 *L. edwardsi* (7 , 18) for *L. harlandii*, 15 *L. edwardsi* (6 , 9) for *C. oleifera*, and 7 *L. edwardsi* (2 , 5) for *C. axillaris*, respectively. After the experiments, all experimental animals were released at the capture locations.

Statistical analyses

All statistical analyses were performed using Graphed prism 9.3. The one-way ANOVA was used to test for differences in seed hoarding fate and cache size between five seed species by *L. edwardsi*. The independent samples t-test was used to assess the significant differences in hoarding preference and cache size between two seed species by *L. edwardsi*. The correlation of cache size with seed traits and seed fate was analyzed using simple linear regression. The variables were log-transformed to meet the assumptions of the statistical models if necessary.

Results

Seed fates of the five tree species manipulated by L. edwardsi

The one-way ANOVA results show that there were no significant differences in the proportion of EIS, IAR, EAR, and LH between five seed species by *L. edwardsi* ($F_{4.51}$ = 0.386, P = 0.817; $F_{4.51}$ = 0.215, P = 0.929; $F_{4.51}$ = 1.060, P = 0.386; $F_{4.51}$ = 0.460, P = 0.758). We found significant differences in seed removal from seed stations and scatter hoarded between the five seed species by *L. edwardsi*, respectively ($F_{4,51}$ = 6.650, P < 0.001; $F_{4,51}$ = 5.511, P < 0.001; Fig. 1).

The independent samples t-test results show that there were significant differences in the scatter-hoarded preference between *C. axillaris* and *C. henryi*, *C. oleifera*, *Q. variabilis*, and *L. harlandii* by *L. edwardsi*, respectively (t = 4.182, df = 22, P < 0.001; t = 5.158, df = 17, P < 0.0001; t = 3.312, df = 18, P = 0.004; t = 2.586, df = 12, P = 0.024; Fig. 1).

Cache size of the five tree species manipulated by L. edwardsi

There were 443, 340, 281, 257 and 34 caches of *L. harlandii*, *C. henryi*, *C. oleifera*, *Q. variabilis*, *C. axillaris* established by *L. edwardsi*, respectively, with an average cache size of 1.52 ± 0.38, 1.33 ± 0.31, 1.92 ± 0.54 1.40 ± 0.33, and 2.06 ± 1.27 (mean ± SD). The one-way ANOVA results showed that there was a significant difference in the cache size between five seed species by *L. edwardsi* ($F_{4,72}$ = 3.985, P = 0.006; Fig. 2). The independent samples t-test results showed that there were significant differences in the cache size between *C. henryi and C. axillaris*, *C. henryi* and *C. oleifera, C. oleifera* and *Q. variabilis, C. oleifera* and *L. harlandii* by *L. edwardsi*, respectively (t = 2.127, df = 22, P = 0.045; t = 3.754, df = 30, P < 0.001; t = 2.936, df = 26, P = 0.007; t = 2.655, df = 38, P = 0.012; Fig. 2). There were no significant differences in the cache size between *C. oleifera* and *C. axillaris*, *Q. variabilis* and *C. axillaris, L. harlandii* and *C. axillaris, C. henryi* and *Q. variabilis, Q. variabilis* and *L. harlandii, L. harlandii* and *C. axillaris* (all P > 0.05; Fig. 2).

Correlation of cache size with seed fates of L. edwardsi

Correlation analysis results show that cache size was not significantly correlated with the proportion of IIS, EIS, EAR, SH, and LH (r = 0.591, P = 0.294; r = 0.016, P = 0.979; r = 0.337, P = 0.579; r = -0.567, P = 0.319; r = 0.339, P = 0.576; Fig. 3A, B, D, E, F). However, cache size was significantly positively correlated with the proportion of IAR (r = 0.915, P = 0.029; Fig. 3C).

Correlation of seed traits with the cache size of L. edwardsi

Correlation analysis results show that cache size was significantly negatively correlated with seed mass (r = -0.925, P = 0.025; 4A) and crude starch (r = -0.975, P = 0.005; Fig. 4B). However, there was a significant positive correlation between cache size and crude fat (r = 0.961, P = 0.009; Fig. 4C).

We found that cache size was not significantly correlated with the content of crude protein, crude fiber, tannin, and caloric value (r = 0.800, P = 0.104; r = 0.811, P = 0.096; r = -0.632, P = 0.253; r = 0.777, P = 0.122; Fig. 4D, E, F, G).

Discussion

In this study, we utilized a combination of five seed species to quantitatively evaluate the correlation between seed traits, seed fates, and cache size of *L. edwardsi.* Our results showed that there were significant differences in the scatter-hoarded preference among *C. axillaris*, *C. henryi*, *C. oleifera*, *Q. variabilis* and *L. harlandii* by *L. edwardsi.* There was a significant difference in the cache size between five seed species by *L. edwardsi*. More importantly, we found that there was a significant positive correlation between cache size and the proportion of IAR or crude fat, but a significant negative correlation between cache size and seed mass or crude starch.

Previous findings have indicated that seeds that require more time and effort to handle, as well as those with higher nutritional value, are at a greater risk of being harvested and stolen by rodents in enclosures (Hou et al. 2021). In this study, we found that *C. henryi* seeds with the largest seed mass and crude starch were more likely to be harvested and scatter-hoarded after removal by *L. edwardsi*, consistent with previous findings (Chang and Zhang 2014). Our results also showed that seeds of *C. axillaris* with lower crude starch, tannin and the highest seed coat thickness, crude protein, crude fiber, and calorific value were less likely to be harvested and hoarded by *L. edwardsi.* Therefore, we propose that the concept of high handling time is subjective. If the energy required for handling time does not yield a sufficient return, the animal may choose to decrease or completely abandon the collection and storage of those particular seeds (Vander Wall et al. 2018). Seeds of high value are actively selected and scatter hoarded, but are also rapidly pilfered from the caches (Vander Wall 2008). The value of one seed species can influence the fate of other seed species that are available at the same time (Lichti et al. 2014). Studies have shown that larger cache sizes mean more high-value food for rodents (Yi et al. 2021). Seeds with a higher fat content were preferentially selected by rodents (Jansen et al. 2004). Studies also found that seed choice was related to the environment and that squirrels appear to consider more traits when caching seeds than when choosing to consume seeds (Sundaram et al. 2018). These results indicated that different seed traits affect the hoarding behavior and seed fate of *L. edwardsi.*

Previous studies have shown that the calorific value and the crude starch per seed affected the strategies and behaviors of seed hoarding of rodents (Chang and Zhang 2014; Wang et al. 2014). Our results indicated that *C. oleifera* seeds with lower tannin were more likely to scatter-hoarded by *L. edwardsi.* Therefore, the results of the hoarding of five seed species by *L. edwardsi* fail to support the hypothesis of high nutrition in semi-natural enclosures. Our study revealed a significant correlation between cache size and seed mass, as well as crude fat and crude starch. It is possible that the seed mass may lead to differences in the intensity of odors emitted by the scatter-hoarded sites, thus affecting the searching behavior of rodents with olfactory signals as the main foraging cues (Chen et al. 2022). This suggests that larger seeds may be more attractive to rodents, as they provide a stronger scent and more sensory information. Additionally, larger seeds may be more nutritious and provide a greater energy source for rodents. (Niu et al. 2011), and the greater the probability of seed theft (Li et al. 2018). Among the five seed species, the seed mass of the *Q. variabilis* and *C. henryi* seeds was relatively large and the cache size was smaller after being dispersed by *L. edwardsi*. The crude starch content of *Q. varialilis, L. harlandii and C.*

henryi was higher and the cache sizes were smaller. The crude fat content of *C. oleifera* and *C. axillaris* was higher and the cache size was also larger. Previous studies indicated that cache size is directly related to the nutritional value of scatter-hoarded sites. Finding large caches means that more food can be obtained, and rodents tend to look for large caches and caches with high nutritional value. Large seeds and seeds with a high fat content are often preferred by rodents (Jansen et al. 2004). However, our results showed that the crude protein, crude fiber, calorific value, and tannin were not significantly correlated with the cache size of *L. edwardsi*. The cache size changed with the variation in seed mass, which may be one of the adaptive strategies of rodents to avoid seed theft from competitors.

Previous research on *Tamias sibiricus* has shown that chipmunks have a higher rate of discovering caches when the cache size is larger (Liu et al. 2016). The proportion of cached seeds of *T. sibiricus* was found to increase with larger cache sizes (Zhang and Zhang 2006). Studies also showed that seeds with higher crude fat content had larger cache size, and rodents tended to seek scatter-hoarded sites with higher nutritional value, such as the proportion of *L. edwardsi* finding high-fat *C. oleifera* was significantly higher than that of *Q. serrata*, *C. glauca*, and *Q. varialilis* (Xiao and Zhang 2004). In our study, we found that the cache size of *L. edwardsi* is closely related to the nutritional value of seeds. Seeds rich in fat are more likely to be associated with large cache size, while seeds rich in starch are more likely found in small caches. High-fat seeds in food storage sites can provide more energy return for rodents, while the starch content of seeds is generally associated with the chemical defense of seeds (Zhang et al. 2016). There is a negative correlation between the cache size and the starch content of the seeds. This suggests that there may be a trade-off between energy input and nutrient return in the establishment of food hoarding sites.

In addition, we found that caches containing a single seed accounted for the highest proportion of all food caches of *L. edwardsi*. Among them, *C. henryi* (78%), *Q. varialilis* (73%), *L. harlandii* (68%), *C. axillaris* (58%), *C. oleifera* (52%). Previous studies showed that most of the food hoarding sites of rodents (78.6%) contained only a single seed of *Q. varialilis* (Chang et al. 2008). *Sciurotamias davidianus* seed hoarding experiments (Zhang et al. 2015) showed that the cache size of *Armeniaca sibirica* in food hoarding sites was 1–3, while the cache size of *Juglans regia* and *Amygdalus davidiana* was one. Our results showed that no matter how the seed characteristics changed, rodents generally chose to store a single seed in a cache. Larger cache sizes are more likely to be recovered by the hoarder, but the risk of pilfering was consistently high by the same or different species of rodents (Yi et al. 2021). Resource competition among large cache sizes is not conducive to the formation and establishment of seedlings. Establishing smaller food-hoarding sites can effectively reduce the pilfering risk. For plants, the smaller the cache size, the higher the dispersal degree of seeds, which not only facilitates the long-distance dispersal of seeds but also improves the seedling establishment. Thus, rodents prefer to establish a single seed hoarding site, which reduces the seed density, is conducive to plant germination and the establishment of seedlings, but also reduces the pilfering risk by other predators, which is a kind of reciprocity between animals and plants.

In conclusion, our results indicated that seed traits, especially seed mass, crude fat, and crude starch, are important factors in influencing the cache size of *L. edwardsi*. When several seed species with various seed traits are available simultaneously, rodents must consider trade-offs between seed traits, in turn, affect seed fate and cache size. Rodents not only need to improve the recovery rate of food hoarding sites, but also effectively reduce the pilfering risk of cache food, so as to obtain more returns from food hoarding sites. Establishing food storage sites based on different seed traits involves a trade-off between the recovery rate and the pilfering rate of food-hoarding sites, which may be an adaptive storage strategy formed in the long-term evolution process.

Declarations

Author contribution

X. Yi conceived and designed the experiments. M. Wang performed the experiments. M. Wang and X. Yang analyzed the data. All authors wrote and revised the manuscript.

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Data availability

All data generated or analysed during this study are included in this published article.

Data accessibility statement

Data generated and analyzed during this study are available at Figshare and can be accessed at https://doi.org/10.6084/m9.figshare.22721065

Ethical approval

The behavioral studies (including live trapping, handling, transport, housing, and experimental studies) were complied with the legal requirements of China and were approved by Ethical Committee of Qufu Normal University.

Conflict of interest

All authors declare no conflict of interest.

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Figures

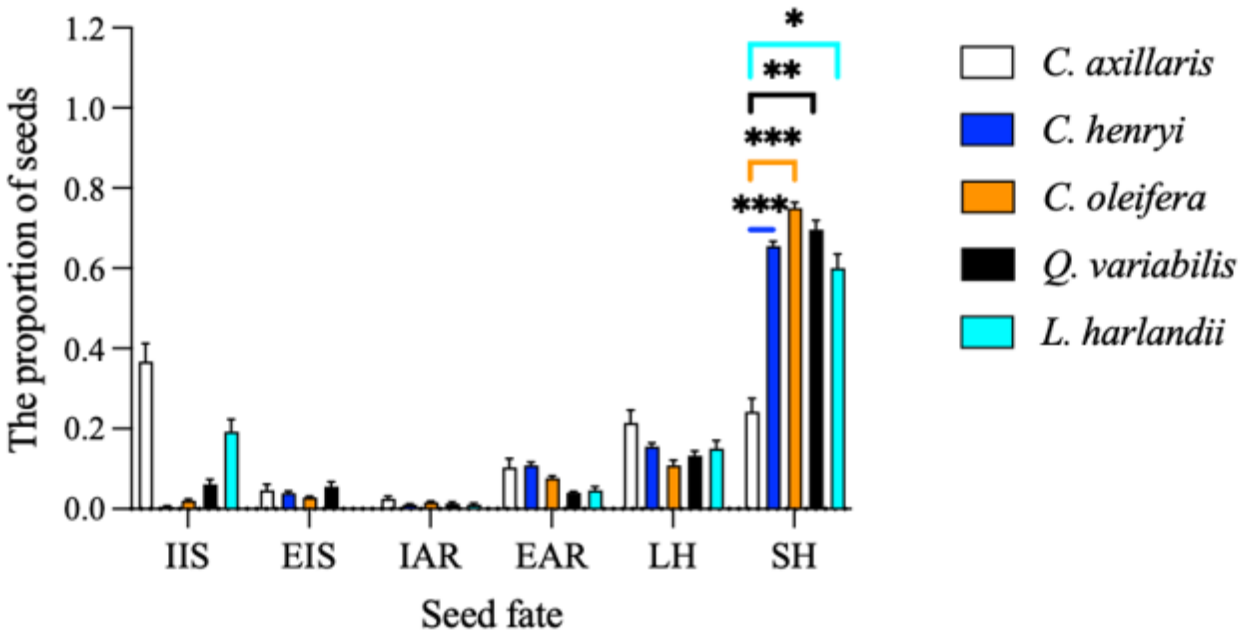


Figure 1

Seed fates of the five tree species manipulated by *L. edwardsi* (Mean ± SE). IIS, intact in situ; EIS, eaten in situ; IAR, intact after removal; EAR, eaten after removal; SH, scatter-hoarded in the shallow pits; LH, larder-hoarded in the nesting boxes. *, **, and *** indicate a significant difference between the two seed species at levels of $P < 0.05$, 0.01, and 0.001, respectively.

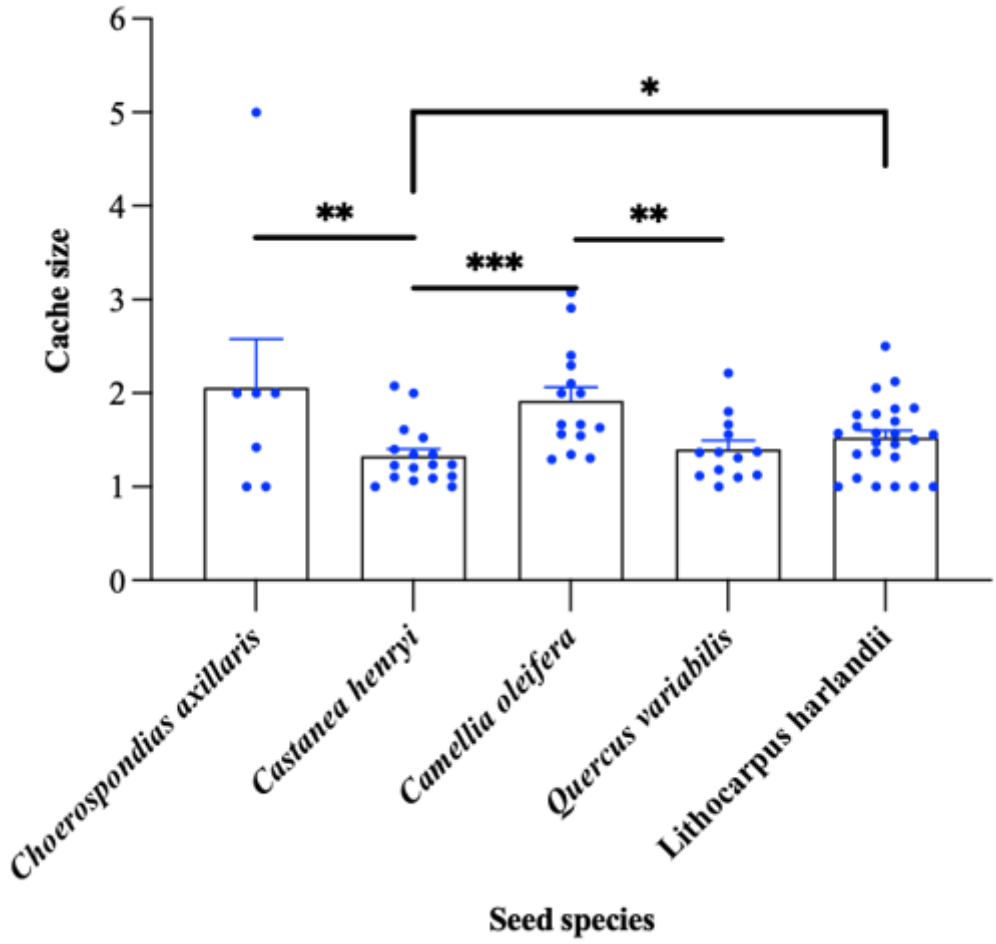


Figure 2

Cache size of the five seed species manipulated by *L. edwardsi* (mean ± SE). *, **and *** indicate a significant difference between the two types of seed at levels of $P < 0.05$, 0.01 and 0.001, respectively.

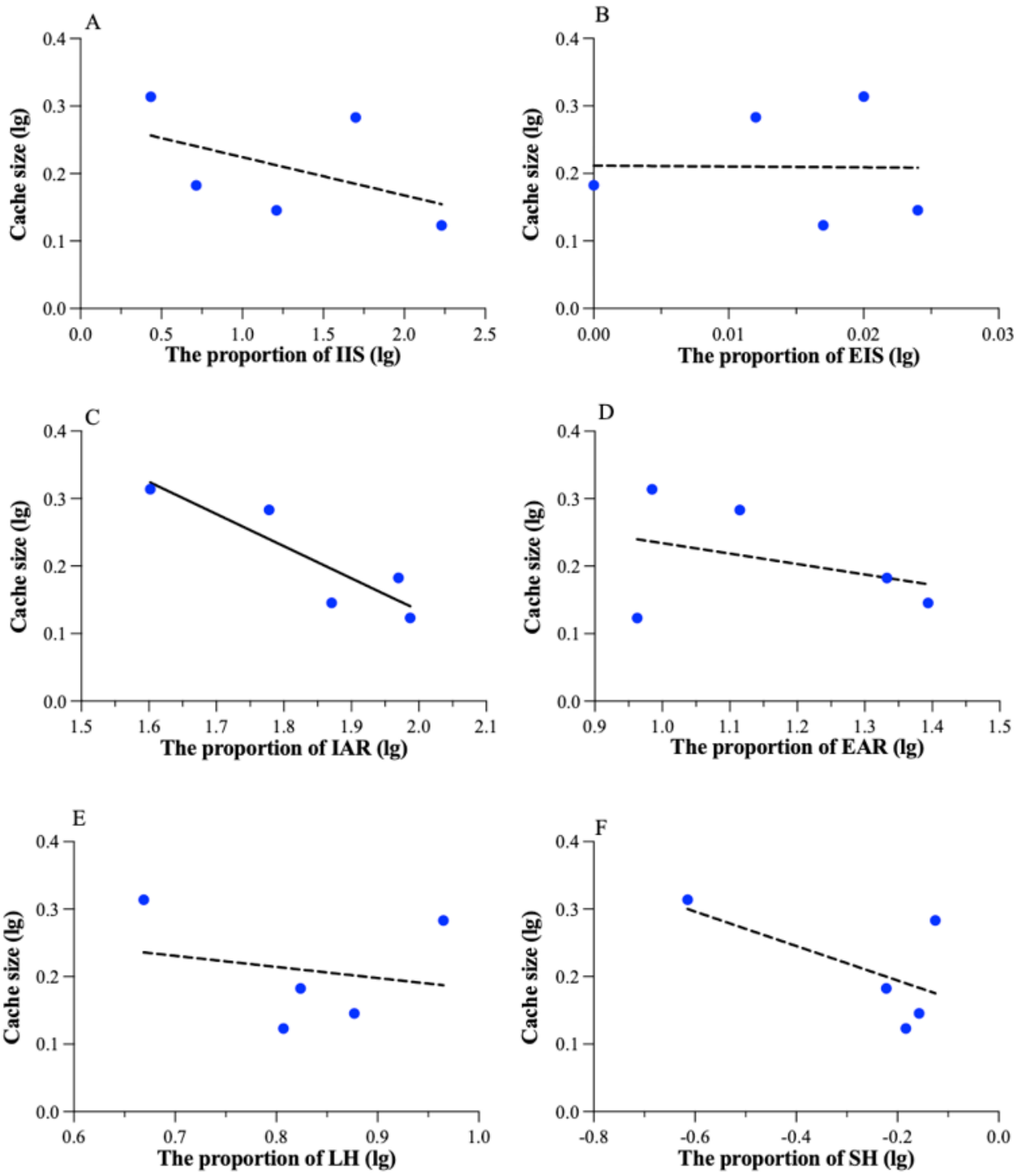


Figure 3

Correlation of cache size of *L. edwardsi* with seed fates. IIS, intact in situ (**A**); EIS, eaten in situ (**B**); IAR, intact after removal(**C**); EAR, eaten after removal (**D**); LH, larder-hoarded in the nesting boxes (**E**); SH, scatter-hoarded in the shallow pits (**F**). The significant relationship is shown by a solid trend line (P <0.05).

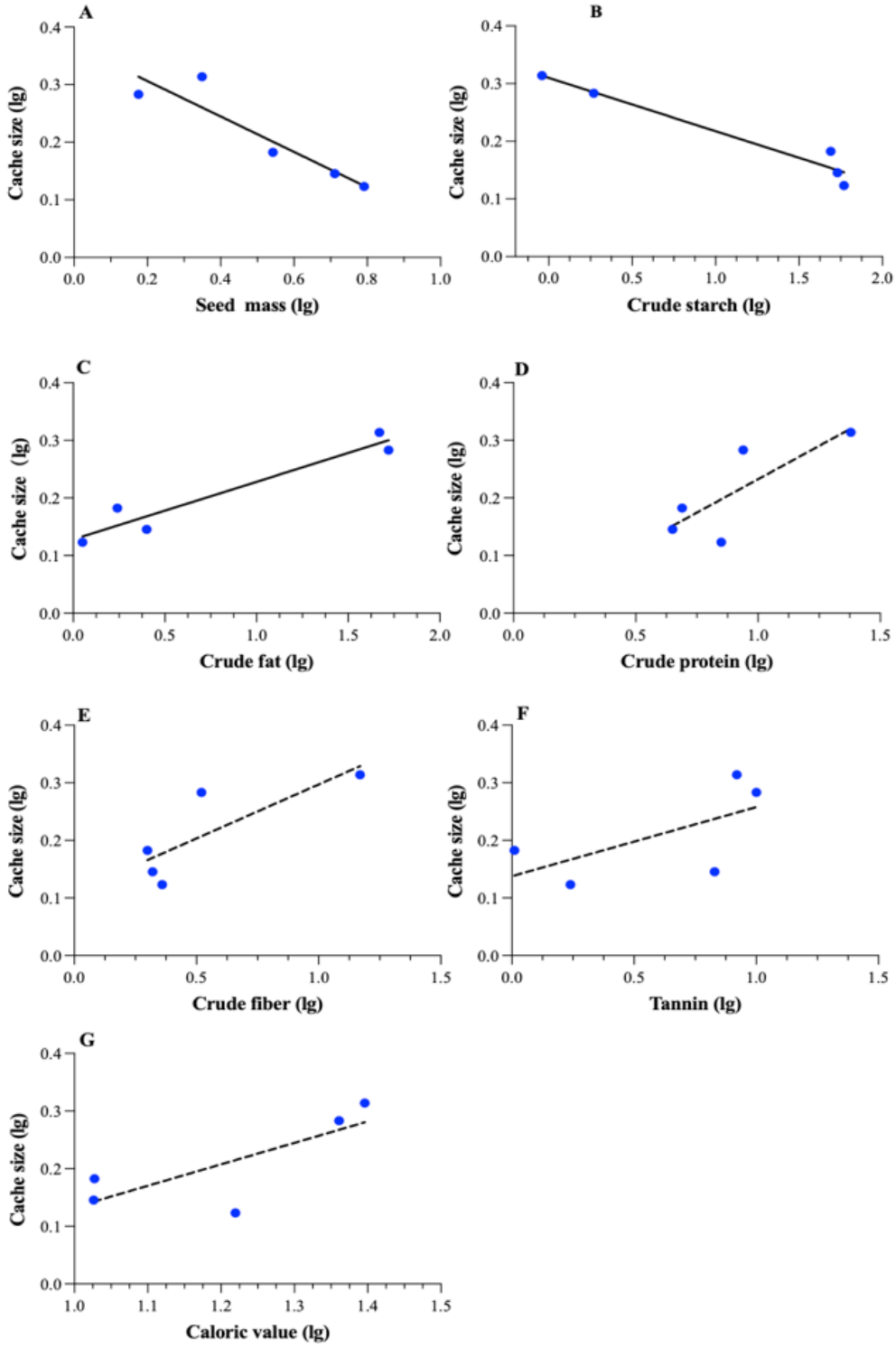


Figure 4

The correlation of cache size of *L. edwardsi* with seed fresh mass (**A**), the content of the crude starch (**B**), crude fat (**C**), crude protein (**D**), crude fiber (**E**), tannin (**F**), and the caloric value of the seeds (**G**). The significant relationship is shown by a solid trend line (P <0.05).