



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* in semi-natural enclosures in Dujiangyan, southwest China, in an attempt to elucidate the relationship between seed traits and cache size. Significant differences were detected in the scatter-hoarding preference of *L. edwardsi* for seeds of *C. axillaris*, *C. henryi*, *C. oleifera*, *Q. variabilis*, and *L. harlandii*. There was a significant difference in the cache size between the five seed species made by *L. edwardsi*. More importantly, we found that there was a significant positive correlation between the cache size and crude fat but a significant negative correlation between cache size and seed mass as well as crude starch. Our study has revealed that seed traits appear to be a key factor in regulating the hoarding behavior of rodents, mainly the size of their caches. This regulation, in turn, has a significant impact on seed survival and seedling establishment 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 species on the hoarding behavior of rodents. How seed traits affect cache size and subsequent seed fate mediated by hoarding rodents remains unknown. This study systematically illustrates how rodents manipulate seed fates and manage cache size according to seed traits. Managing cache size based on different seed traits involves a trade-off between cache recovery and pilferage, which may be an evolutionary strategy of scatter-hoarding animals.

Keywords *Leopoldamys edwardsi* · Food hoarding · Seed fate · Seed traits · Cache size

Introduction

The cache size refers to the number of seeds buried in each cache when an animal stores seeds (Lu et al. 2004). During seed caching, 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 on the ground (Yang et al. 2023). Previous studies have 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.

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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 such 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 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), while rodents show better memory on the large seeds with high nutritional value than small ones 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 (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 chemical defense (Jansen et al. 2004; Chang et al. 2009; Vander Wall 2010). Studies have also shown that rodents put more spatial memory on cached seeds with weak odors and tend to scatter-hoard seeds with weak odors (Yi et al. 2016; Li et al. 2018).

Previous studies show that fox squirrels (*Sciurus niger*) usually store single black walnuts (*Juglans nigra*) in each storage site (Stapanian and Smith 1984; Hayashida 1988; Lee 2002). Eurasian red squirrel (*Sciurus vulgaris*), however, buries 1~11 *Pinus koraiensis* seeds in a single cache (Yahner 1975; Hurley and Robertson 1987). The yellow pine chipmunks (*Tamias amoenus*) often bury 1~22 seeds of *Pinus jeffreyi* in each cache (Vander Wall 1995). Caches of white-footed mice (*Peromyscus leucopus*) often contain 25~30 seeds of North American arbor pine (Abbott and Quink 1970). A large cache size containing more seeds will emit a stronger odor signal (Johnson and Jorgensen 1981), which is helpful for rodents to find the stored seeds (Jiang 1996; Liu et al. 2016). On the other hand, large-sized caches may be at high risk of pilferage (Yi et al. 2016; Vander Wall et al. 2018; Yang et al. 2023). In these scenarios, both hoarding animals and seeds they handle may have a potential to affect the number of seeds in caches, i.e., cache size. However, few studies have evaluated the relationship between seed traits and cache size of scatter-hoarding rodents.

Therefore, 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, 2018;

Xiao et al. 2015; Meng et al. 2022). Scatter-hoarding rodents adjust the cache size based on the seed traits of the seeds they store (Jansen et al. 2004; Zhang et al. 2016). Furthermore, the cache size made by rodents indirectly determines the establishment, competition, and survival of seedlings (Vander Wall et al. 2009; Xiao et al. 2015). Thus, studies of the effects of seed traits on the cache size of rodents not only provide an in-depth understanding of the scatter-hoarding behavior of rodents but also reveal the co-evolutionary relationship between rodents and plant seeds (Xiao and Zhang 2004; Yang et al. 2018, 2022), which plays a key role in maintaining local seed dispersal and plant regeneration (Xiao et al. 2005, 2006; Cheng et al. 2005a).

The Edward's long-tailed, *Leopoldamys edwardsi*, the dominant scatter-hoarding species in the subtropical evergreen broad-leaved forest in the Dujiangyan region, consumes and caches a variety of plant seeds, such as *Quercus variabilis*, *Quercus serrata*, *Lithocarpus harlandii*, and *Camellia oleifera* (Xiao and Zhang 2004; Yang et al. 2018, 2022), and plays an important role in maintaining local seed dispersal and plant regeneration (Xiao et al. 2006, 2008; Cheng et al. 2005a, b; Xiao 2022). A large number of studies have focused on a certain seed trait of a single species (Cheng et al. 2005b; Chang et al. 2008) or the effect of a certain seed trait of several species 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 using seeds of *Castanea henryi*, *Q. variabilis*, *L. harlandii*, *C. oleifera*, and *Choerospondias axillaris*.

Materials and methods

Study site

This experiment was carried out at the Banruosi Experimental Forest in Dujiangyan, Sichuan Province (altitude 700~1000 m) from September to December 2018. The Dujiangyan region (30°45'~31°22'N, 107°25'~103°47'E), belonging to the Sichuan Basin, is the transition zone from the Qinghai-Tibet Plateau to the Chengdu Plain. 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 an annual sunshine duration of 800~1000 h and annual average relative humidity of more than 80%. The major vegetation type is a natural secondary forest dominated by *Q. variabilis*, *Q. serrata*, *Lithocarpus hancei*, *Cyclobalanopsis glauca*, *C. axillaris*, and *C. oleifera* (Yang et al. 2018, 2022).

Castanea henryi is the dominant tree species in a nearby forest in the Qingcheng Mt, ca. 20 km from the Banruosi Experimental Forest (Xiao et al. 2008). 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).

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. All individuals of *L. edwardsi* were kept in separate cages in the lab after their 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 individuals were selected for the seed hoarding experiment.

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). Two nest boxes (40 cm × 40 cm × 40 cm) were placed in the two opposite corners of each enclosure, and an appropriate amount of wood chips was provided to keep the rodents warm. Two drinking pans were placed near the nest boxes to provide *L. edwardsi* with drinking water during the behavioral experiments. During the experiment, a certain number of seeds of each species were placed in the seed station for *L. edwardsi* to store or consume, depending on the seed mass of each species.

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 trees, 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 values in this study were extracted from previous studies in this region (Xiao et al. 2008; Yang et al. 2020; Table 1).

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) was inserted into a small hole (1.5 mm in diameter) drilled on each seed. We ensured that the PIT tag would not fall off during seed handling by rodents. This marking method is different from the plastic tag marking commonly used in previous studies and has little influence on the experiments (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 tagged seeds of one 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 g; mean \pm SD), 40 for *L. harlandii* (3.487 ± 0.795 g), 50 for *C. oleifera* (1.499 ± 0.348 g), 40 for *Q. variabilis* (5.145 ± 0.940 g), and 40 for *C. henryi* (6.183 ± 0.887 g), depending on seed mass of each species. The next morning at 07:00, *L. edwardsi* was moved out of the enclosure, and all shallow pits were scanned individually with a hand-held reader (Model RBC-S03, Anhui Raybaca IoT Technology Co., Ltd., China) to record how many tagged seeds were cached by *L. edwardsi*. 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 tagged seeds in the caches were detected. Cache size refers to the number of seeds that were buried in each pit by *L. edwardsi*. Seed fates were categorized into (1)

Table 1 Seed traits of the five seed species used in this study ($n=50$)

Seed traits	<i>Quercus variabilis</i>	<i>Lithocarpus harlandii</i>	<i>Camellia oleifera</i>	<i>Choerospondias axillaris</i>	<i>Castanea henryi</i>
Seed fresh mass mean \pm SD (g)	5.14 ± 0.94	3.49 ± 0.80	1.50 ± 0.35	2.23 ± 0.35	6.18 ± 0.89
Crude protein (%)	4.43	4.92	8.63	23.77	7.05
Crude fat (%)	2.54	0.58	52.92	46.48	1.11
Crude starch (%)	49.50	53.70	1.87	0.92	58.71
Crude fiber (%)	2.08	1.98	3.32	14.86	2.31
Tannin (%)	6.69	0.97	0.10	0.12	0.57
Caloric value (KJ/g)	10.62	10.65	22.96	24.88	16.58

Seed traits of *C. henryi* are from Xiao et al. (2008); Seed traits of *C. axillaris*, *L. harlandii*, *C. oleifera*, and *Q. variabilis* are from Yang et al. (2020)

intact in situ (IIS): tagged seeds remained at the seed station, (2) eating in situ (EIS): tagged seeds were eaten at the seed station, (3) intact after removal (IAR): the rodents removed the tagged seeds from the seed station and discarded them on the enclosure floor, (4) eaten after removal (EAR): the rodents removed the tagged seeds from the seed station and then consumed, (5) larder-hoarded (LH): tagged seeds stored in the nest boxes, (6) scatter-hoarded (SH): tagged seeds were cached in the shallow pits. After that, all residual seeds and rodent feces were cleaned for another batch of hoarding experiments. It was not possible to record data blind because our study involved focal animals in the field.

In this study, the caching activity of 12 *L. edwardsi* (6 ♀, 6 ♂) was recorded for seeds *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. For each seed species, each animal was used only once. However, we excluded the animals that did not eat or cache any seeds in this study, possibly because seeds of some tree species are not attractive to 7 *L. edwardsi*, e.g., *C. axillaris*. After the experiments, all experimental animals were released at the capture locations.

Statistical analyses

All statistical analyses were performed using Graphed Prism 9.3, SPSS 26.0, and R (R Core Team 2022). Because the number of seeds placed in seed stations during the hoarding experiments was inconsistent, we used the proportion of seeds to compare seed fates. The one-way ANOVA was used to test for the differences in seed fates between five seed species. Post-hoc analysis was used to assess the significant differences in hoarding preference between two seed species. The linear mixed models were used to test the differences in cache sizes between five seed species, with rodent ID as a random factor. Moreover, we also used a likelihood ratio test to measure the significance of the fixed effects (the Anova function in R package “car”). Significant differences in cache sizes between different seed species were evaluated by least-squares means (the pairs function in R package “emmeans”). The correlation of cache size with seed traits was analyzed using Pearson correlation analysis.

Results

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

The one-way ANOVA results showed that there were no significant differences in the proportion of EIS ($F_{4,51} = 0.386$, $P = 0.817$; Fig. 1B), IAR ($F_{4,51} = 0.215$,

$P = 0.929$; Fig. 1C), EAR ($F_{4,51} = 1.060$, $P = 0.386$; Fig. 1D), and LH ($F_{4,51} = 0.469$, $P = 0.758$; Fig. 1E) between five seed species. We found significant differences in the proportion of IIS and SH between the five seed species ($F_{4,51} = 6.650$, $P < 0.001$; Fig. 1A; $F_{4,51} = 5.511$, $P = 0.001$; Fig. 1F).

The post-hoc analysis showed that significant differences in the proportion of IIS between *C. axillaris* and *C. henryi* ($P < 0.001$; Fig. 1A), *C. axillaris* and *C. oleifera* ($P < 0.001$; Fig. 1A), *C. axillaris* and *Q. variabilis* ($P < 0.001$; Fig. 1A), *C. henryi* and *L. harlandii* ($P = 0.020$; Fig. 1A), and *C. oleifera* and *L. harlandii* ($P = 0.042$; Fig. 1A; Appendix Table S1). There were significant differences in the proportion of SH between *C. axillaris* and *C. henryi* ($P < 0.001$; Fig. 1F), *C. axillaris* and *C. oleifera* ($P < 0.001$; Fig. 1F), *C. axillaris* and *Q. variabilis* ($P < 0.001$; Fig. 1F), and *C. axillaris* and *L. harlandii* ($P = 0.008$; Fig. 1F; Appendix Table S1).

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

In total, 443, 340, 281, 257, and 34 caches of *L. harlandii*, *C. henryi*, *C. oleifera*, *Q. variabilis*, and *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 \pm SD). The linear mixed models showed a significant difference in the cache size between five seed species by *L. edwardsi* ($\chi^2 = 13.476$, $df = 4$, $P = 0.009$; Fig. 2). Further analysis showed that there were significant differences in the cache size between *C. henryi* and *C. axillaris* ($t = -2.695$, $df = 48.529$, $P = 0.010$), *C. henryi* and *C. oleifera* ($t = -2.964$, $df = 44.620$, $P = 0.005$), *C. axillaris* and *Q. variabilis* ($t = 2.049$, $df = 44.347$, $P = 0.046$), respectively, but there were no significant differences in the cache size between other seed species pairs (all $P > 0.05$; Fig. 2; Appendix Table S2).

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

Correlation analysis showed that cache size was significantly negatively correlated with seed mass ($r = -0.925$, $P = 0.025$; Fig. 3A) and the content of seed crude starch ($r = -0.975$, $P = 0.005$; Fig. 3C). However, there was a significant positive correlation between cache size and the content of seed crude fat ($r = 0.961$, $P = 0.009$; Fig. 3B).

Cache size was not significantly correlated with the content of crude protein ($r = 0.800$, $P = 0.104$; Fig. 3D), crude fiber ($r = 0.811$, $P = 0.096$; Fig. 3E) and tannins ($r = -0.632$, $P = 0.253$; Fig. 3F), and caloric value ($r = 0.777$, $P = 0.122$; Fig. 3G).

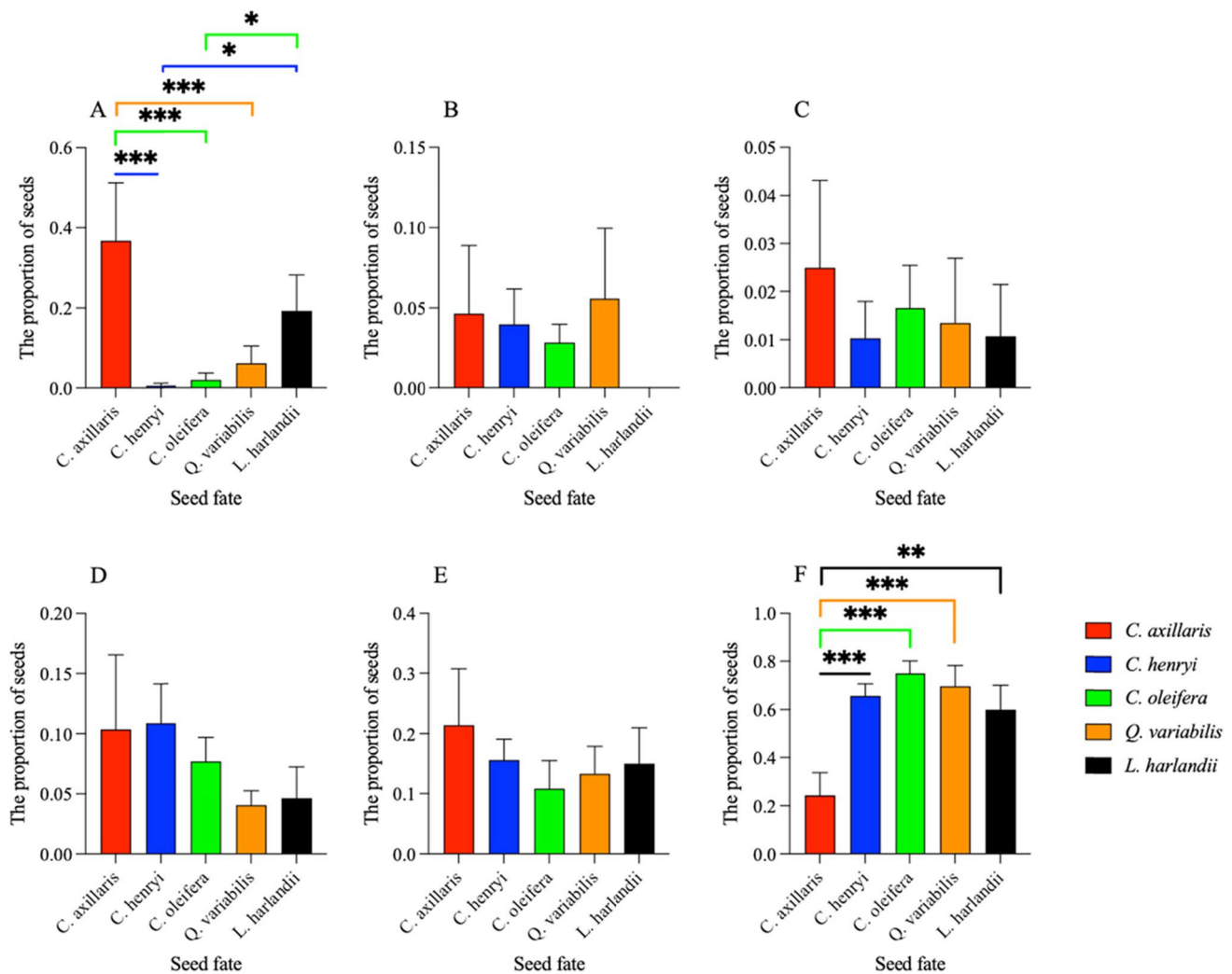


Fig. 1 Seed fates of the five tree species manipulated by *L. edwardsi* (mean \pm SE). **A** IIS, intact in situ; **B** EIS, eaten in situ; **C** IAR, the rodents removed the seeds from the seed station and discarded them on the enclosure floor; **D** EAR, the rodents removed the seeds from the seed station and consumed them on the enclosure floor; **E** LH, larder-

hoarded in the nesting boxes; **F** SH, scatter-hoarded in the shallow pits. *, **, and *** indicate a significant difference between the two seed species at levels of $P < 0.05$, 0.01, and 0.001, respectively

Discussion

Seed traits play a key role in manipulating the scatter-hoarding behavior of rodents (Vander Wall 1995, 2003; Xiao et al. 2005; Sundaram et al. 2018; Yang et al. 2023). There is much evidence that rodents balance energy expenditure and gain during storage (Stapanian and Smith 1984; Yang et al. 2023), e.g., preferring large seeds with high energy value for storage and small seeds with low energy value for feeding (Jansen et al. 2004; Zhang et al. 2008; Chang et al. 2009; Chen and Chen 2011; Pesendorfer et al. 2016; Wang and Yi 2022). Our study using *L. edwardsi* presents further evidence that scatter-hoarding rodents prefer to store seeds of *Q. variabilis*, *L. harlandii*, *C. henryi*, and *C. oleifera* that are either large in size or rich in fat content. On the contrary, seeds of

C. axillaris are less likely to be stored by *L. edwardsi* mainly because of their low profitability and high physical defense. This difference reflects the fact that scatter-hoarding rodents trade off their hoarding and feeding strategy based on the physical and chemical traits of seeds (Longland and Dimitri 2018; Zalamea et al. 2018; Wang and Yi 2022).

The amount of seeds in a single cache not only determines cache recovery rates by scatter-hoarding rodents that rely on both spatial memory and olfaction but also affects cache pilferage by naïve animals that mainly use olfaction to pilfer the stored seeds (Yi et al. 2016; Cao et al. 2018; Wang and Yi 2022). The seed number in caches may lead to differences in the seed odor intensity, thus affecting the search efficiency of rodents with olfactory signals as the main foraging cues (Chen et al. 2022). For example, *Tamias*

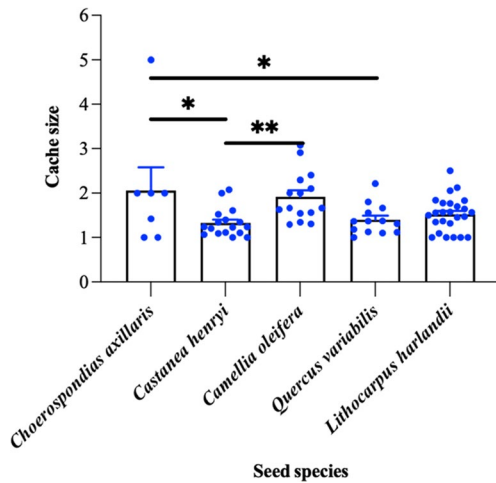


Fig. 2 Cache size of the five seed species manipulated by *L. edwardsi* (mean ± SE). * and ** indicate a significant difference between the two types of seed at levels of $P < 0.05$ and 0.01 , respectively

sibiricus have a higher cache recovery rate when the cache size is large (Zhang and Zhang 2006; Liu et al. 2016). Moreover, the seed number in caches represents energy rewards to both hoarders and pilferers. Therefore, the number of seeds in caches may reflect a hoarding strategy adopted by rodents to balance cache recovery and cache pilferage. Our results showed that there was a significant difference in the cache size between the five seed species manipulated by *L. edwardsi*, indicating the important role of seed traits in determining the cache size of scatter-hoarding animals.

In this study, we found that there was a significant positive correlation between cache size and crude fat, whereas a significant negative correlation between cache size and seed mass as well as crude starch. However, the concentration of seed crude protein, crude fiber, and tannins as well as seed caloric value failed to explain the variations in cache size of *L. edwardsi*. This demonstrates that not all seed traits play an

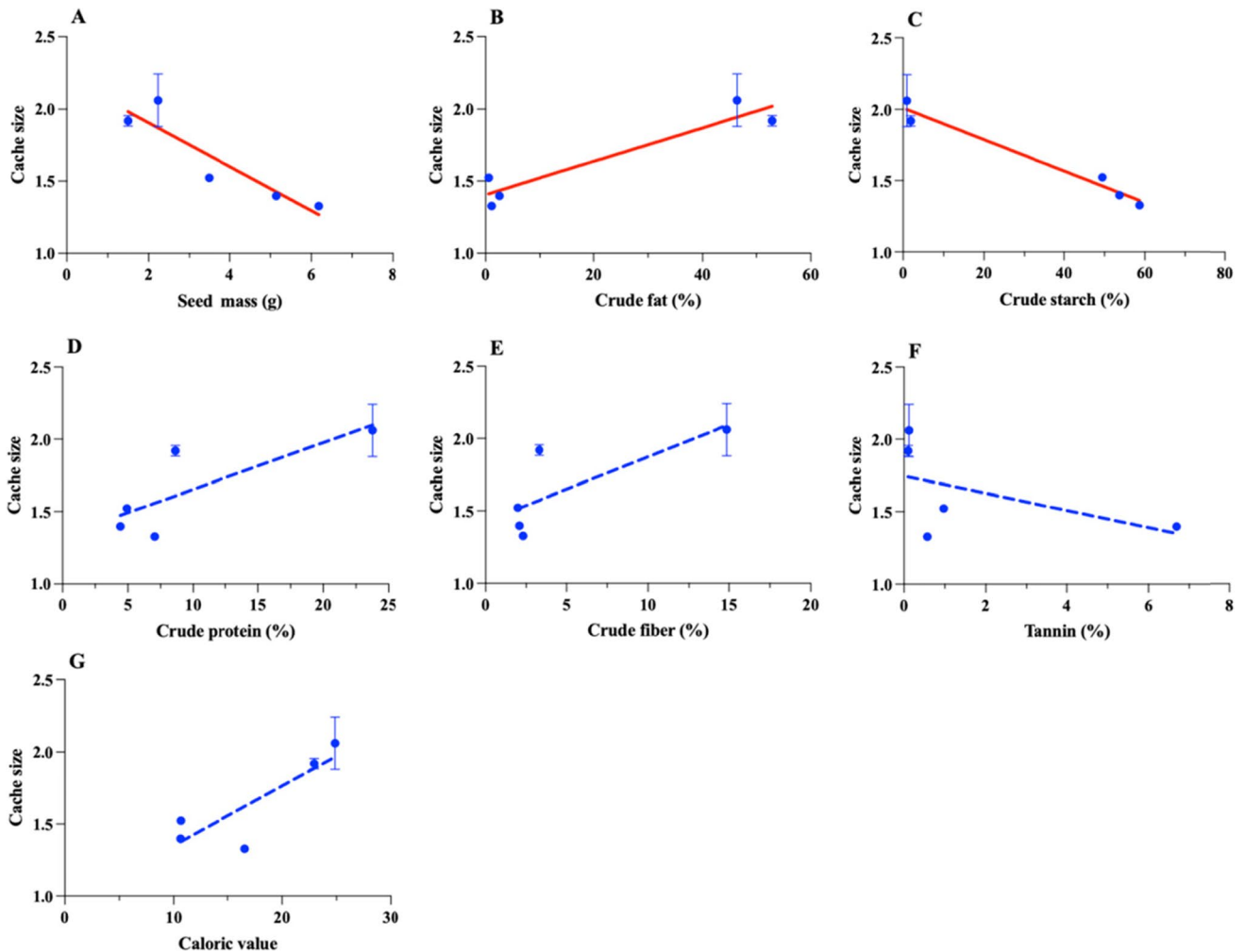


Fig. 3 The correlation of cache size of *L. edwardsi* with seed mass (A), the content of the crude fat (B), crude starch (C), crude protein (D), crude fiber (E) and tannin (F), and the caloric value of tree spe-

cies (G). Solid trend lines stand for significant relationship at $P < 0.05$ level. Cache size was expressed as mean ± SD for each tree species

important role in affecting the cache size of food-hoarding animals. Seeds rich in fat usually contain high energy (Zhang et al. 2016; see Appendix Fig. S1); therefore, storing more high-fat seeds in a single cache will provide more rewards to the hoarding rodents. The content of seed starch is generally associated with chemical defense (Zhang et al. 2016), and establishing small-sized caches may reflect the low profitability of high-starch seeds. While rewards from caches are unable to explain the negative relationship between cache size and seed mass. This can be explained by the fact that seed mass is not necessarily related to seed calorific values (Yang et al. 2012; see Appendix Fig. S2). Moreover, storing large-sized seeds in small caches is expected to reduce cache pilferage by sympatric competitors. Although seed tannins and caloric values affect hoarding behavior (Xiao and Zhang 2004), no significant effects are detected on cache size, possibly because of the distant genetic relationship of the seed species in this study. Despite this, the correlation of cache size to seed traits may represent one of the adaptive strategies of scatter-hoarding rodents to gain more rewards from their caches. This suggests that there is a trade-off between energy input and nutrient return in the establishment of caches by food-hoarding animals.

Although cache size is closely related to seed traits, caches containing one single seed accounted for a large proportion of caches made by *L. edwardsi* in our study, i.e., *C. henryi* (78%), *Q. variabilis* (73%), *L. harlandii* (68%), *C. axillaris* (58%), and *C. oleifera* (52%). Our results showed that no matter how the seed traits change, *L. edwardsi* often bury a single seed in most of their individual caches. These results are consistent with previous studies showing that most caches (78.6%) of hoarding rodents contained single seed of *Q. variabilis* (Chang et al. 2008) and *Armeniaca sibirica* (Zhang et al. 2015). Caches made by scatter-hoarding rodents *Sciurotamias davidianus* consistently contain a single seed of *Juglans regia* or *Amygdalus davidiana* (Zhang et al. 2015). Previous studies have shown that larger cache sizes are more likely to be recovered by the hoarder (Zhang and Zhang 2006; Liu et al. 2016); however, the risk of pilferage remains consistently high by the same or different species of rodents (Li et al. 2018; Yi et al. 2021). Therefore, establishing small-sized caches is expected to be an evolutionary strategy of scatter-hoarding rodents to balance reward gain and food loss from their caches. From the perspective of plants, a small cache size means a high level of seed dispersal, more opportunity for survival, and high potential for seedling establishment. Thus, seed trait-mediated cache size management may represent an adaptive strategy of plants to increase their seed dispersal fitness, which reflects the mutualistic relationship between plants and food-hoarding animals.

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 scatter-hoarding

rodent *L. edwardsi*. When several plant species with varying seed traits are available simultaneously, rodents must consider trade-offs between seed traits, which 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 by manipulating their cache size, so as to obtain more returns from caches.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03379-7>.

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

Declarations

Ethical approval The behavioral studies (including live trapping, handling, transport, housing, and experimental studies) complied with the legal requirements of China and were approved by the Ethical Committee of Qufu Normal University. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Conflict of interest The authors declare no competing interests.

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