# Seed dispersal of three sympatric oak species by forest rodents in the Qinling Mountains, Central China

**Gang Chang · Tiezhi Jin · Junfeng Pei · Xiaoning Chen · Bo Zhang · Zijun Shi**

**Abstract** Forest rodents play an essential role as seed dispersal vectors through their caching behaviors. Using seeds of *Quercus aliena*, *Q. glandulifera*, and *Cyclobalanopsis engleriana* (Fagaceae), which are dominant, but poorly studied species, in the Qinling Mountains, Central China, we investigated seed predation and dispersal by forest rodents in 2010 and 2011. There were significant differences in rodent seed-eating and caching strategies among the three tree species. Seeds of *Q. aliena* and *C. engleriana* had hard coats, high nutrition contents (e.g., protein, fat, and starch), and long germination schedules (*C. engleriana* only). They were less frequently eaten in *situ*, but more likely to be eaten after removal or cached. Seeds of *Q. glandulifera* had soft coats and low nutrition contents and were more often eaten in *situ* and less likely to be eaten after removal or cached. Our findings indicated that forest rodents were primarily responsible for seed predation and dispersal of these three tree species in the Qinling Mountains, and seed traits, especially coat hardness, nutrition content, and germination schedule, were important factors influencing rodent eating and caching behaviors. In addition, seed dispersal process of each tree species differed significantly between the 2 years, reflecting the effect of mast seeding on the eating and caching strategies of forest rodents.

**Keywords** Fagaceae trees · Forest rodents · Seed caching · Seed traits · Mast seeding

## Introduction

Seed dispersal is a key phase affecting plant regeneration, species survival, and distribution (Howe and Smallwood 1982). By acting as seed vectors, granivorous rodents play an essential role in the dispersal phase through their scatter-hoarding behaviors. Although rodents consume a large number of seeds for energy, they also store some seeds in well-spaced scatter caches (one seed per cache) (e.g., Stapanian and Smith 1984) for future use, such as winter survival or during reproduction. Buried seeds are more likely to germinate and survive to become seedlings than seeds on the surface (Vander Wall 2001). Thus, both the animals and the seeds appear to benefit; if an animal fails to recover some of its cache of seeds, because it has died, moved, or stored more than it could use,

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those seeds could germinate under suitable conditions (Vander Wall 1990; Wenny 2000).

Acorns are an important food source for many wild animals across the Northern Hemisphere (Chang et al. 2009). Much attention has been paid to the dispersal biology of oaks, which are common or dominant tree species in many temperate and tropical forests (Vander Wall 2001; Jansen et al. 2004; Xiao and Zhang 2006; Moore et al. 2007; Zhang et al. 2008). However, our knowledge of the interactions between oaks and animals is still poor in the Qinling Mountains because dispersal is often a complicated, multistage process and because there is great temporal and spatial variation in forest dynamics (Vander Wall 2002a). Although *Quercus aliena*, *Q. glandulifera*, and *Cyclobalanopsis engleriana* (Fagaceae) are dominant species in the Qinling Mountains and contribute substantially to the stability and biodiversity of the forest ecosystem, they are not well studied.

Seed traits, which often co-vary, have an important impact on the eating and hoarding strategies of rodents. For example, Xiao et al. (2006a) investigated the seed predation and removal of six sympatric large-seeded tree species by granivorous rodents. They found that high fat or large seeds were both more likely to be removed and were harvested more quickly than small seeds with high tannin concentrations. The results indicated that innate seed traits were very important to seed dispersal. However, no field evidence exists on whether seed traits affect successful seed dispersal of the oak species *Q. glandulifera*, *Q. aliena,* and *C. engleriana* in the Qinling Mountains.

The main goal of the present study was to investigate seed dispersal in these three oaks species by seed-eating rodents in the Qinling Mountains of Shaanxi Province, Central China. Here, we address two questions: (1) Are seed-eating rodents effective dispersal agents for these three oaks species? and (2) Which seed traits are most closely correlated to seed dispersal by scatter-hoarding rodents?

## Methods

### Study site and study species

This study was conducted during successive autumns (September–November) in 2010 and 2011 in the

Foping National Nature Reserve (35°0′N, 105°30′E) located on the south aspects of the Qinling Mountains of Shaanxi Province, Central China. The Qinling Mountains are situated in the transitional zone between two macroclimatic regimes (i.e., subtropical and warm-temperate zones), making them a biologically rich area and sensitive to climatic change. Annual precipitation ranges from 950 to 1,200 mm, most of which falls between July and September. Snow cover usually lasts 5 or more months (from November to March), and annual mean temperature ranges from 6 to 11 °C below 2,000 m and from 1 to 6 °C above 2,000 m above sea level (Chen 1983). The natural vegetation types in the Qinling Mountains are deciduous broad-leaved forests (below 2,000 m), mixed conifer and deciduous forests (2,000–2,500 m), and conifer forests (above 2,500 m) (Liu and Zhang 2003). This project focused on deciduous broad-leaved forests, where nut-bearing species, such as *Q. aliena*, *Q. glandulifera*, *Q. variabilis*, *Q. spinosa*, *C. engleriana*, and *Castanea mollissima* are the most common. Three dominant oak species, *Q. aliena*, *Q. glandulifera*, and *C. engleriana*, were used in this study (Table 1). At the study site, several rodent species, including David's rock squirrel (*Sciurotamias davidianus*), Swinhoe's striped squirrel (*Tamiops swinhoei*), the white-bellied rat (*Niviventer confucianus*), the South China field mouse (*Apodemus draco*), and the greater long-tailed hamster (*Tscheskia triton*) (Liu and Zhang 2003; Xiao et al. 2009), rely on acorns and other nuts as important food sources. Of these, white-bellied rats, South China field mice, and David's rock squirrels have been found to scatter hoarded acorns at other study sites (Lu and Zhang 2005; Chang and Zhang 2011).

To survey animals, we used large, wire cage traps (30 cm × 25 cm × 20 cm) baited with peanuts (for food) and cabbage (for water) and provisioned with local dry leaves as nest material. The traps and nesting material protected rodents from cold weather and predators. From August to September of each study year, trapping was conducted at 10 plots in the study site. Forty traps were set 10 m apart along two transect lines in each plot and checked for three consecutive days. Traps were deployed at 19:00 to 19:30 h and checked after 12 h. After taxonomic identification and weighing, all trapped animals were released on site.

**Table 1** Seed traits of the three oak species studied in Foping National Nature Reserve

| Seed species | Fresh weight (g)[a] | Coat hardness (mm)[a] | Crude protein (%)[b] | Crude fat (%)[b] | Crude starch (%)[b] | Tannin (%)[c] | Germination schedule |
|---|---|---|---|---|---|---|---|
| Q. glandulifera | 1.09 ± 0.03 | 0.23 ± 0.004 | 4.69 | 0.86 | 45.0 | 8.76 | 0 (Early) |
| Q. aliena | 1.59 ± 0.04 | 0.31 ± 0.005 | 13.79 | 2.66 | 61.5 | 8.34 | 0 (Early) |
| C. engleriana | 0.91 ± 0.04 | 0.24 ± 0.005 | 8.58 | 1.63 | 56.6 | 8.85 | 1 (Delayed) |

[a] Mean ± SE, $N = 50$

[b] Seed nutrient compositions were measured by the Measurement Center of Northwest A&F University, China (A2011.015)

[c] Seed tannin content was measured by the Center of Grain Quality of Ministry of Agriculture, China (K120042)

Seed traits analyses

Seed physical traits (i.e., fresh weight and coat hardness) were measured by electronic balance and vernier caliper (mean ± SE, $N = 50$ for every species) and chemical traits were measured by professional testing institutions (Table 1). Seed tannin content of dry nutmeat was measured according to the GB/T15686-2008 standard of determination of tannin content in sorghum. Seed protein content of dry nutmeat was measured according to the NY/T3-1982 standard of determination of crude protein content in cereals and legumes (semimicro-Kjeldahl method). Seed fat content of dry nutmeat was measured according to the NY/T3-1982 standard of determination of crude fat content in cereals and oil crops. Seed starch content of dry nutmeat was measured according to the NY/T11-1985 standard of determination of crude starch content in cereals grain.

Experimental procedure

In order to estimate simply the seed production, we selected randomly 10 parent trees of each species to count the seed crops on the ripening and dropping season (about earlier to October) in 2010 and 2011, on the ground of each parent tree, a random plot (1 × 1 m) was established to count the seed quantities (including intact and destroyed seeds). We used these quantitative data as the background of mast seeding.

After the seeds of these three species ripened in 2010 and 2011, we collected fresh acorns from the ground beneath parent trees and used water flotation to distinguish between sound and weevil-damaged or empty seeds. Then, we selected 400 fresh, sound seeds for each species, labeled them with plastic tags following the line-tag method reported by Zhang and Wang (2001), and numbered each tag to identify each seed. Tagging has been shown to have a negligible effect on seed removal and caching by rodents (Xiao et al. 2006b).

Twenty plots (1 × 1 m), spaced 15 m apart along a transect line, were established as seed stations in deciduous broad-leaved forest. In October of each year (2010 and 2011), 20 tagged seeds for each species (60 seeds total) were placed at each station. Seed fates were monitored on days 1, 2, 3, 5, 7, 16, 24, and 162 (the following spring) and were similar for each year. During each visit, we searched the area around each station (radius <15 m) to retrieve those seeds removed by rodents and record their fates (2–4 h for two people each visit). Post-dispersal seed fates could be sorted into five categories: (1) remained intact in *situ* (R); (2) eaten in *situ* (ES); (3) eaten after removal (ER); (4) cached (CA); and (5) removed from *situ* (RS), including ER, CA, and missing seeds.

When a cache was found, we recorded the tag number of the acorns and measured its distance to the source. Then, we use a chopstick which was coded with the same number of the tag to mark the cache location. The chopstick was set 20 cm away from the cache; this method of marking has been shown have no effect on cache retrieve by rodents (Xiao et al. 2006b). During subsequent visits, we checked all caches found on previous visits until the caches had been removed or eaten by rodents. If a marked cache was removed, the area around the cache was searched, to determine whether it had been re-cached or eaten, and the distance to its original source was measured. Primary and secondary cache sites were identified based on the coded number and subsequent movement by rodents.

Statistical analysis

The proportions of remaining, eaten, and cached seeds were arcsine-square-root transformed before statistical

analysis. Independent-sample *t* tests were used to compare the differences in seed production of every seed species between 2010 and 2011. Cox regressions were used to compare the times to removal from seed stations among the three seed species. General linear models were used to test differences in lifetimes of tagged seeds that were eaten in *situ*, eaten after removal, cached, and removed from *situ* among the three seed species with seed species and time as fixed factors. One-way ANOVAs were used to test the differences in dispersal distance of primary and secondary caches among the three seed species. Spearman correlations were used to test the relationships between seed traits and fates of seeds handled by rodents in each of survey time. All statistical analyses were performed by means of R version 2.10.0 (Crawley 2007), and the significance level was set at $P < 0.05$.

## Results

### Rodent abundance

In 2010, we captured 45 rodents; white-bellied rats, David's rock squirrels, and South China field mice were the dominant species and comprised 40.0 %, 28.9 %, and 24.4 % of all captures, respectively. We also captured a small number of Himalayan rats (6.7 %). In 2011, we captured 37 rodents. White-bellied rats, David's rock squirrels, and South China field mice were dominant in this year as well, comprising 40.5 %, 27.0 %, and 24.3 % of all captures, respectively. We also captured a small number of Himalayan (2.8 %) and chestnut rats (5.4 %).

### Mast seeding

There were significant differences in seed crops between 2010 and 2011 for each of these three species ($P < 0.01$, respectively). Few seeds of *Q. aliena* (9.9 ± 0.9), *Q. glandulifera* (9.2 ± 1.1), and *C. engleriana* (8.8 ± 0.8) were found in the plots in 2010, while numerous seeds of all three species (55.2 ± 2.3, 50.5 ± 2.1, and 47.5 ± 1.9, respectively) were found in 2011.

### Seed dispersal and seed fates

In 2010, there were no significant differences in seed lifetime at the stations among the three tree species

(Wald = 0.00, $df = 2$, $P = 1.00$); all seeds were removed (eaten or cached) from seed stations after 2 days. In 2011, seed lifetimes at stations were much longer than in 2010. Seed lifetime of *Q. glandulifera* at seed stations was significant longer than that of *Q. aliena* and *C. engleriana* and there were significant differences in seed lifetimes among these three species (Wald = 84.686, $df = 2$, $P < 0.001$) (Fig. 1).

In 2010, there were no significant differences in ES among the three species ($F = 1.335$, $df = 2$, $P = 0.265$), and their interactions with time also had no significant differences ($F = 0.972$, $df = 14$, $P = 0.483$). Like ES, there were also no significant differences in ER and RS among the three species ($F = 0.088$, $df = 2$, $P = 0.916$ and $F = 1.302$, $df = 2$, $P = 0.274$) and their interactions with time ($F = 0.781$, $df = 14$, $P = 0.690$ and $F = 1.327$, $df = 14$, $P = 0.193$). However, seed cache rates differed significantly ($F = 10.039$, $df = 2$, $P < 0.001$); more seeds of *Q. aliena* and *C. engleriana* were cached than *Q. glandulifera*. But, their interactions with time had no significant differences in CA ($F = 0.355$, $df = 14$, $P = 0.985$); there were nearly same variational trend of caching with time (Figs. 2, 3, 4, 5).

In 2011, these three species differed significantly not only in CA ($F = 48.201$, $df = 2$, $P < 0.001$) but
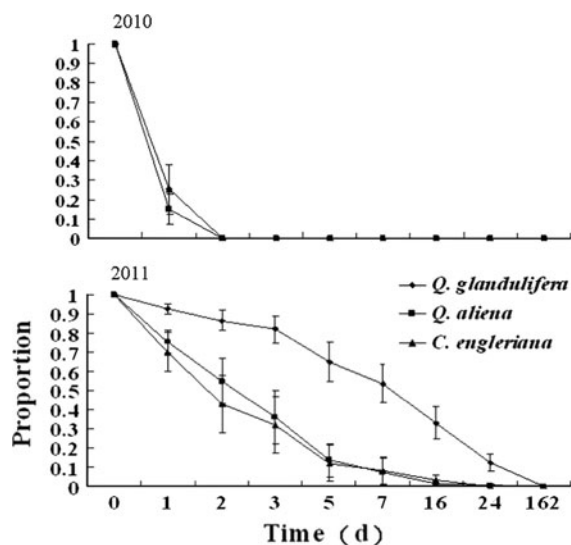


**Fig. 1** Proportions of seeds that remained in *situ* for three oak species (*Q. glandulifera*, *Q. aliena*, and *C. engleriana*) in Foping National Nature Reserve. The denominator of the proportion at each time is the total seed number per species at one station (i.e., 20), and this also applies equally to Figs. 2, 3, 4 5
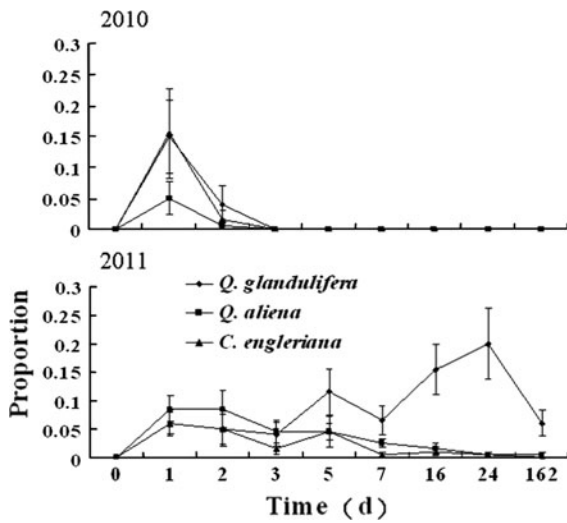
**Fig. 2** Proportions of seeds that were eaten in *situ* for three oak species (*Q. glandulifera*, *Q. aliena*, and *C. engleriana*) in Foping National Nature Reserve
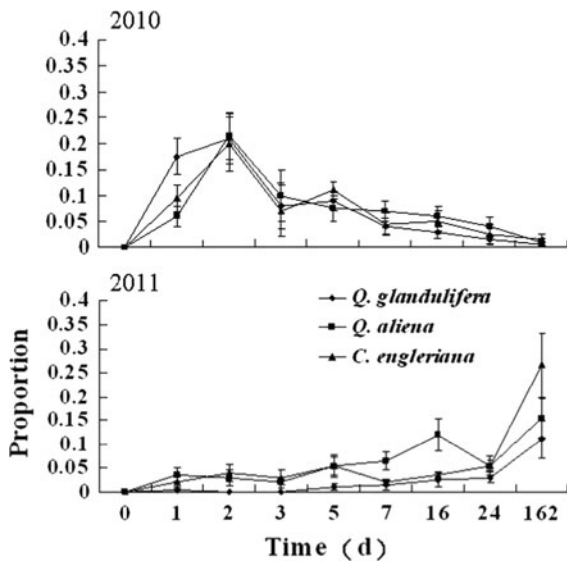


**Fig. 3** Proportions of seeds that were eaten after removal for three oak species (*Q. glandulifera*, *Q. aliena*, and *C. engleriana*) in Foping National Nature Reserve



**Fig. 4** Proportions of seeds that were cached for three oak species (*Q. glandulifera*, *Q. aliena*, and *C. engleriana*) in Foping National Nature Reserve



**Fig. 5** Proportions of seeds that were removed from *situ* for three oak species (*Q. glandulifera*, *Q. aliena*, and *C. engleriana*) in Foping National Nature Reserve

also in ES ($F = 17.191$, $df = 2$, $P < 0.001$), ER ($F = 14.272$, $df = 2$, $P < 0.001$), and RS ($F = 4.952$, $df = 2$, $P < 0.01$). Similar to 2010, more seeds of *Q. glandulifera* were eaten in *situ* or after removal, while more seeds of *Q. aliena* and *C. engleriana* were cached. Their interactions with time also had significant differences in ES ($F = 3.070$, $df = 14$, $P < 0.001$), ER ($F = 1.912$, $df = 14$, $P = 0.026$),
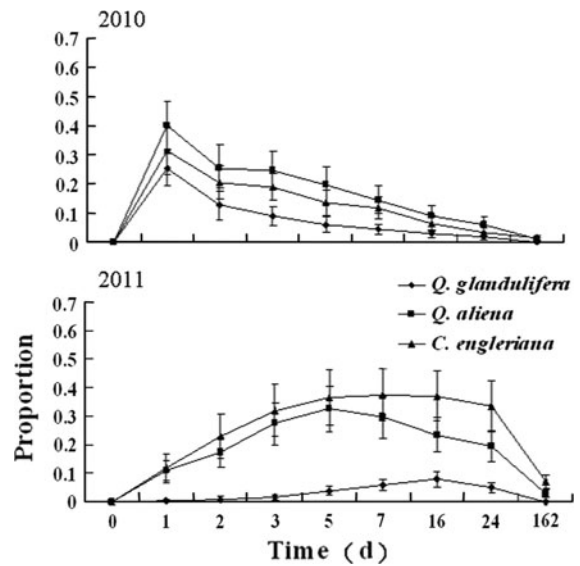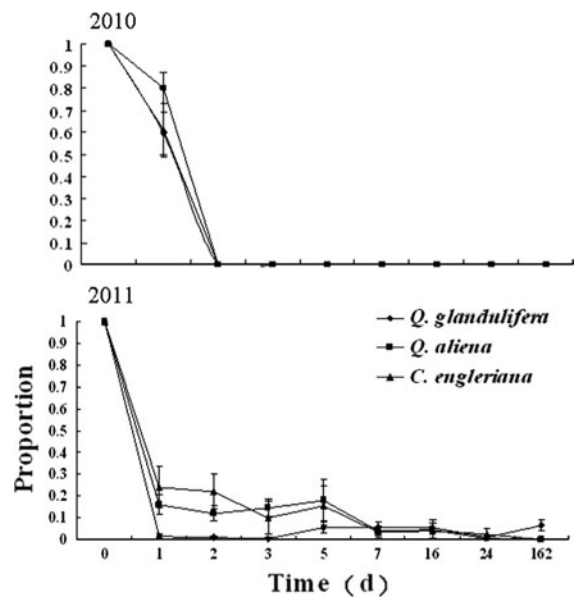
and RS ($F = 1.726$, $df = 14$, $P = 0.05$), but had not significant differences in CA ($F = 0.946$, $df = 14$, $P = 0.510$) (Figs. 2, 3, 4, 5).

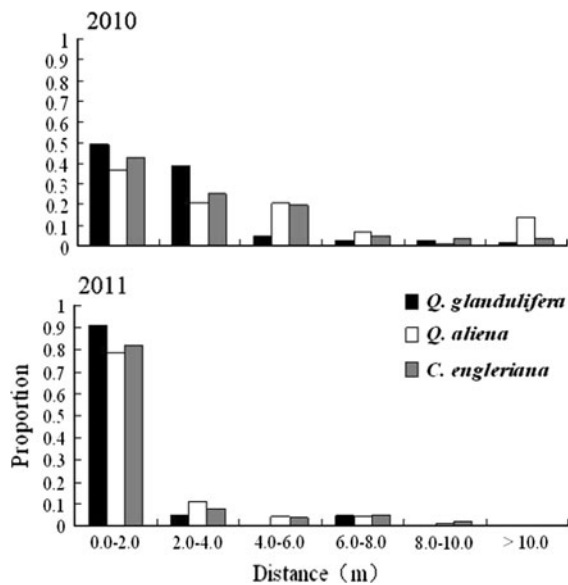All removed seeds, including eaten and cached seeds, were distributed within 15 m of seed stations

**Fig. 6** Proportional distributions of the three oak species over different primary caching distances



**Fig. 7** Proportional distributions of the three oak species over different secondary caching distances

for all three species. The average primary caching distances were 2.59 ± 0.31, 5.13 ± 0.55, and 3.71 ± 0.56 m for seeds of *Q. glandulifera*, *Q. aliena*, and *C. engleriana*, respectively, and were significantly different ($F = 5.931$, $df = 2$, $P = 0.003$) in 2010. The average secondary caching distances were 5.45 ± 1.22, 11.16 ± 1.79, and 8.57 ± 2.03 m, respectively, for the three species and were not significantly different ($F = 2.558$, $df = 2$, $P = 0.082$) (Fig. 6). In 2011, the average primary caching distances were 0.93 ± 0.33, 1.59 ± 0.22, and 1.54 ± 0.21 m for seeds of *Q. glandulifera*, *Q. aliena*, and *C. engleriana*, respectively, and were not significantly different ($F = 0.097$, $df = 2$, $P = 0.378$). The average secondary caching distances were 0.8 ± 0.72, 1.91 ± 0.56, and 2.33 ± 0.81 m, respectively, and were not significantly different ($F = 0.203$, $df = 2$, $P = 0.817$) (Fig. 7).

### Effect of seed traits on seed fates

Both seeds that remained in *situ* and seeds that were eaten in *situ* showed significant negative correlations with coat hardness, protein, fat, starch, and germination schedule ($P < 0.01$). Seeds that were eaten after removal showed significant positive correlations with coat hardness, protein, fat, and starch ($P < 0.05$). Seeds that were cached showed significant positive
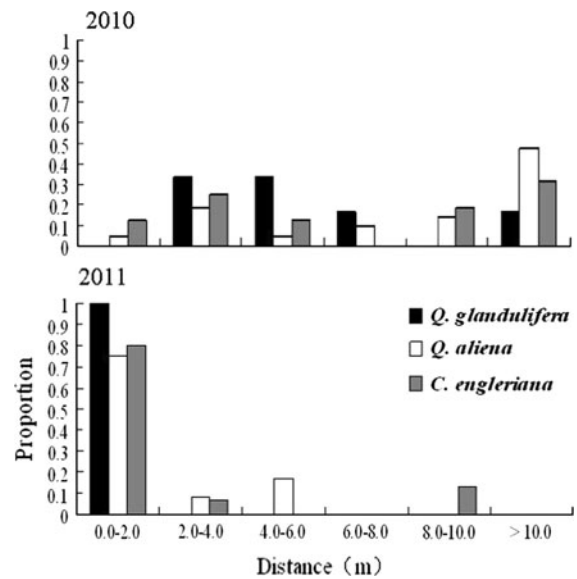
correlations with coat hardness, protein, fat, starch, and germination schedule ($P < 0.01$) (Table 2). These results indicate that seeds with hard handled trait (i.e., heavy weight or hard coat) tended to be less frequently remained in *situ* and eaten in *situ*, but more frequently eaten after removal and cached by rodents. Seeds with high nutritional traits (i.e., high protein, high fat, and high starch) also are less frequently remained in *situ* and eaten in *situ*, more frequently eaten after removal and cached by rodents. Seeds with long germination schedule are less frequently remained in *situ* and eaten in *situ*, and more frequently cached by rodents.

### Discussion

In this study site in the Qinling Mountains, forest rodents were primarily responsible for seed predation and dispersal. However, there were significant differences in rodent eating and caching strategies among the three species *Q. glandulifera*, *Q. aliena*, and *C. engleriana*. First, although seed lifetime in *situ* did not differ among species in 2010, it was significantly longer for seeds of *Q. glandulifera* than seeds of *Q. aliena* and *C. engleriana* in 2011; in that year, few seeds of *Q. glandulifera* were eaten or removed before the 3rd day. Moreover, small numbers of *Q. glandulifera* seeds still remained at the release

**Table 2** Correlations between seed traits and seed fates of seeds handled by rodents

| Seed traits | Average time to remained in *situ* | Average time to eaten in *situ* | Average time to eaten after removal | Average time to cached | Average time to removed from *situ* |
|---|---|---|---|---|---|
| Fresh weight | 0.044 | 0.099 | 0.054 | −0.024 | 0.048 |
| Coat hardness | −0.289** | −0.219** | 0.153* | 0.399** | 0.094 |
| Crude protein | −0.289** | −0.219** | 0.153* | 0.399** | 0.094 |
| Crude fat | −0.289** | −0.219** | 0.153* | 0.399** | 0.094 |
| Crude starch | −0.289** | −0.219** | 0.153* | 0.399** | 0.094 |
| Tannin | −0.044 | −0.099 | −0.054 | 0.024 | −0.048 |
| Germination schedule | −0.217** | −0.240** | 0.026 | 0.258** | −0.001 |

* Correlation was significant at the 0.05 level (2-tailed)

** Correlation was significant at the 0.01 level (2-tailed)

stations after 24 days (Fig. 1). Seed lifetime in *situ* directly reflected the seed preferences of rodents, and longer seed lifetime indicated that rodents did not prefer to eat or remove those seeds (Yi and Zhang 2008).

Second, post-dispersal fates of seeds handled by rodents could be categorized as eaten in *situ*, eaten after removal, and cached in this study. Although there were slight differences in seed fates between 2010 and 2011 among these three tree species, the seed fates for each tree species were basically consistent between the 2 years. For seeds of *Q. glandulifera*, the proportion of eaten seeds (including eaten in *situ* and eaten after removal) was higher than that of the other two tree species in both years, but the proportion of cached seeds was lower. Moreover, more seeds of *Q. glandulifera* were eaten in *situ* with time history, while more seeds of *Q. aliena* and *C. engleriana* were removed from *situ* with time history in 2011 (Figs. 2, 3, 4, 5). These results indicated that rodents preferred to disperse seeds of *Q. aliena* and *C. engleriana*.

Finally, dispersal distances were another important index reflecting the preferences of rodents for seeds. According to the predictions of optimal cache spacing models (Stapanian and Smith 1978; Clarkson et al. 1986), scatter-hoarding animals prefer to cache higher-value foods relatively farther away, while lesser-value foods are cached nearer the resource. In this study, the mean caching distances (including primary and secondary caching distances) of *Q. glandulifera* seeds were the shortest in both years (although the differences were only significant in 2008), while the mean caching distances of *Q. aliena* and *C. engleriana* seeds were not significantly

different from one another (Figs. 5, 6). The differences in caching distances among these three species indicated that rodents valued the seeds of *Q. aliena* and *C. engleriana* more highly.

In this study, there were significant differences in the fates (e.g., eaten, cached and dispersal distance) of seeds of these three species between the 2 years. Taking into account the relatively stable population of rodents, these differences may have resulted from mast seeding by the trees. Mast seeding is a common phenomenon in nut-bearing tree species in temperate and tropical forests (Sork 1993; Vander Wall 2001; Kelly and Sork 2002) in which large seed crops in some years are interspersed with greatly reduced seed crops in other years (Jansen et al. 2004). Many studies have shown that mast seeding affects the seed dispersal strategies of rodents (Jansen and Forget 2001; Vander Wall 2002b; Xiao et al. 2005b). For example, Xiao et al. (2005b) found that the proportion of *Castanopsis fargesii* (Fagaceae) seeds that was removed was significantly lower in a masting year than in a low-seed year, while the proportion which was cached was significantly higher. In our study site, the three species produced very few seeds in 2010, and rodents had to consume large numbers of seeds quickly to meet their daily energy needs, leading to rapid seed removal and a reduction in storage. The seed yields of all three species were very high in 2011 (from the background data in seed masting); there were sufficient seeds not only to meet the daily energy needs of rodents but also to cache seeds for future use, resulting in relatively slow removal of these seeds. Likewise, differences in dispersal distances between the 2 years were also influenced by mast seeding.

As optimal cache spacing models predict (Stapanian and Smith 1978, 1984; Clarkson et al. 1986), when seed crops were abundant, the rodents initially cached seeds near the resources then gradually relocated them to farther locations. Therefore, over the short term, the dispersal distances were shorter in the high-seed year than in the low-seed year.

Seed characteristics commonly co-vary in nature. Different plant species have different seed traits (e.g., size, coat hardness, nutrition content, etc.), and these traits influence the behavioral strategies (e.g., eat or cache) of rodents (Chang et al. 2009). Some previous studies have indicated that seed size (Vander Wall 2003, Xiao et al. 2005a, 2006a; Wang and Chen 2009; Chang et al. 2009), coat hardness (Jacobs 1992; Zhang and Zhang 2008; Chang et al. 2010), nutrition content (Smallwood and Peters 1986; Lewis 1982; Izhaki 2002), tannin (Smallwood and Peters 1986; Steele et al. 1993; Xiao et al. 2008; Wang and Chen 2008), and germination schedule (food perishability) (Hadi-Chikh et al. 1996; Steele et al. 2001, 2006; Xiao et al. 2009) may be primary factors which affect the eating and caching strategies of rodents. In this study, seeds of *Q. aliena* and *C. engleriana* with hard coats, high nutrition contents (e.g., protein, fat and starch), and long germination schedules (*C. engleriana* only) tended to be eaten *in situ* less often and were more likely to be eaten after removal or cached, while seeds of *Q. glandulifera* with soft coats and low nutrition contents were more often eaten *in situ* and less likely to be eaten after removal or cached. Because there was no significant difference in tannin content among these three seed species, tannin content did not show significant effect on seed fates (Table 1).

These results indicate that seed coat hardness, nutrition content, and germination schedule are more likely to increase scatter-hoarding, which benefits seedling establishment (Hollander and Vander Wall 2004). With an increase in seed endocarp thickness, rodent handling time increases (Jacobs 1992). This would increase predation risk in the field (Chang et al. 2010). This speculation is supported by the negative correlation between the proportion of seeds eaten in *situ* and seed coat hardness (Table 2). Highly nutritional (e.g., high protein, fat, and starch) seeds are also more likely to be dispersed by rodents because they may be more important in securing a food supply in varying environments (Lewis 1982; Izhaki 2002). This prediction is supported by the positive correlation

between the proportions of seeds cached or eaten after removal and seed nutrition content (Table 2). Germination schedule may also be an important factor affecting the behavioral strategies of seed-eating rodents (Hadi-Chikh et al. 1996; Steele et al. 2001, 2006; Xiao et al. 2009). In this study, although *C. engleriana* seeds were smaller in size and had softer coats and lower nutrition contents than *Q. aliena* seeds, they were more likely to be cached due to their longer germination schedule.

Our results suggested that forest rodents have significant impacts on tree regeneration of large-seeded tree species in the Qinling Mountains. In this study, all cached seeds were shallowly buried (about 3–5 cm deep) in the soil, where temperature and humidity were highly suitable for seedling establishment (Hollander and Vander Wall 2004). Furthermore, about 88 % of caches contained only one seed, and a high proportion of one-seed caches correlate to a lower risk of seed predation and pilferage, lower sibling competition, and higher potential seedling establishment (Forget 1996). After 162 days (i.e., the next spring) in both 2010 and 2011, we found that 1 % (in 2010) and 3 % (in 2011) of the cached *Q. aliena* seeds and 1.5 % (in 2010) and 7 % (in 2011) of the cached *C. engleriana* seeds had survived to the seedling stage. We did not find cached seeds which were damaged by winter desiccation. Although these seedling proportions were not high, given the tens of thousands of acorns produced by each tree annually, the caching behavior of rodents is likely to significantly contribute to seed survival and seedling establishment in natural conditions.

In conclusion, our study found that forest rodents were primarily responsible for predation and dispersal of seeds of *Q. glandulifera*, *Q. aliena*, and *C. engleriana* in the Qinling Mountains. There were significant differences among tree species in the seed-eating and caching strategies of rodents; seeds of *Q. aliena* and *C. engleriana* were more likely to be eaten after removal or cached, while seeds of *Q. glandulifera* were more often eaten *in situ*. Our results indicate that seed traits, especially coat hardness, nutrition content, and germination schedule, are important factors influencing the seed-eating and caching behaviors of rodents. In addition, there was a significant difference in seed dispersal of these three species between the 2 years, reflecting the effect of mast seeding on the seed-eating and caching strategies of forest rodents.

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