Seed-hoarding of Edward’s long-tailed rats *Leopoldamys edwardsi* in response to weevil infestation in cork oak *Quercus variabilis*

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**Abstract** Seed hoarders show different hoarding and eating responses towards insect-infested seeds that can affect the fitness of both the seeds and insects. It remains unclear how seed hoarders adopt different strategies in eating and hoarding infested seeds with and without larvae concealed inside. Here we investigated hoarding and eating responses of Edward’s long-tailed rats *Leopoldamys edwardsi* (scatter hoarders) to weevil infestation of cork oak *Quercus variabilis* seeds within outdoor enclosures. We provided sound seeds, larvae-emerged seeds, (infested seeds where larvae have emerged) and larvae-concealed seeds (infested seeds with larvae concealed inside) to subjects independently (each seed type presented separately) and in pairwise combinations (sound and larvae-emerged seeds; sound and larvae-concealed seeds). We found that *L. edwardsi* removed, scatter hoarded and ate fewer larvae-emerged seeds than sound seeds. No difference was found between sound seeds and larvae-concealed seeds. These results suggest that sound and larvae-concealed seeds are more favored by *L. edwardsi* than larvae-emerged seeds. We posit that not only plants but also insects may benefit from the behavioral responses of hoarders to seed infestation under natural conditions [Current Zoology 57 (1): 50–55, 2011].

**Key words** Larvae survival, Seed discrimination, Seed-hoarding, Seed dispersal, Weevil infestation

It is well recognized that the properties of seeds are important in determining seed-hoarding behavior in hoarders (Dearing et al., 2000; Shimada, 2001; Izhaki, 2002; Vander Wall, 2003; Ganesh and Davida, 2005; Zhang et al., 2008a). As one group of pre-dispersal predators of seeds, insects may affect seed dispersal of plants through damaging seeds and making them less attractive to seed-eating animals (Semel and Andersen, 1988; Andersen and Folk, 1993; Steele et al., 1996; Leiva and Fernández-Alés, 2005; Gálvez and Jansen, 2007). Under natural conditions, small rodents eat more infested seeds *in situ* and remove more sound seeds from seed stations for hoarding. This response may not only benefit dispersal and survival of sound seeds (Oorschot, 2003; Xiao et al., 2003a), but also benefit the control of insects when insect larvae are eaten along with infested seeds (Andersen and Folk, 1993; Steele et al., 1996; Gálvez and Jansen, 2007).

Seed hoarders may exhibit different responses to infested seeds in hoarding and eating (Steele et al., 1996). Some species of mammals and birds can accurately discriminate between sound seeds and infested seeds and prefer to consume infested seeds immediately and hoard sound seeds for future use (Steele et al., 1996; Dixon et al., 1997; Oorschot, 2003). These different strategies may not only affect plant fitness, but also affect insect fitness; however, the latter has been largely ignored (but see Steele et al., 1996). Seed hoarders may respond differently to seeds at different stages of larval infestation such as larvae-concealed seeds and larvae-emerged seeds, and subsequently affect both plant and insect fitness. If infested seeds with larval concealed inside were hoarded as well as sound seeds by hoarders, insects may have higher opportunities of survival. In contrast, if more larvae-concealed infested seeds were eaten before dispersal, insect population growth may be prohibited. Last, if more larvae-emerged seeds were eaten immediately, a greater number of sound seeds and larva-concealed seeds may survive and be dispersed by hoarders which probably increases the fitness of both
plants and insects. Larvae as a protein-rich food complement would compensate for the nutrition loss by infestation and affect behavioral responses of hoarders (Semel and Andersen, 1988; Andersen and Folk, 1993; Silviu, 2002; but see Gálvez and Jansen, 2007).

Here we investigated whether Edward’s long-tailed rats *Leopoldamys edwardsi* (Muridae) prefer or avoid cork oak *Quercus variabilis* (Fagaceae) seeds where larvae have emerged and infested seeds with concealed larvae. Compared with sound seeds, weevil infestation may decrease consumption and hoarding by *L. edwardsi*. Due to the nutritional complement of larvae, larvae-concealed seeds should be favored over larvae-emerged seeds by *L. edwardsi*.

1 Materials and Methods

1.1 Study area

The study was carried out in a subtropical zone (31º45′N, 103º43′E, 700–1000 m a.s.l.) in Dujiangyan, Sichuan province, China. This area is characterized by 1200–1800 mm of annual precipitation, 80% of annual relative humidity, 800–1000 annual sunlight hours and an annual temperature of 15.2°C. *Castanopsis fargesii, Quercus variabilis, Pinus massoniana, Acer catalpifoilum, Camellia oleifera, Quercus serrata, Lithocarpus harlandii, Camellia glauca* and *Phoebe zhenman* are common tree species, but fragmented due to extensive cultivation and logging (Chen, 2000). Among common seed-eating rodents such as *Niviventer fulvescens, Leopoldamys edwardsi, Berylmys bowersi, Niviventer confucians, Rattus nitidus* and *Apodemus latronum, L. edwardsi* is the only species that scatter hoards seeds (Xiao et al., 2002, 2003b; Cheng et al., 2005).

1.2 Experimental animals

Rats were trapped using steel-wire live traps (30 cm × 25 cm × 20 cm) from August to December 2004 (Xiao et al., 2008; Chang et al., 2009). We recorded gender, body weight, age and breeding status and maintained animals in individual plastic boxes (50 cm × 30 cm × 25 cm) at ambient temperature (10–15 °C) and photoperiod (12:12 h light: dark). Commercial mouse chow (*Keao Feed Ltd., Beijing, China*), water and nest substrate were available *ad libitum*. Animals were acclimatized to the laboratory environment at least one week before testing. Tests were carried out during the peak time of seed-hoarding of *L. edwardsi* (September to December 2004, personal observations by Cheng J). Only non-breeding rats were used in experiments. All rats were released at the trap site at the conclusion of our study.

1.3 Seeds collection and marking

Seeds of *Q. variabilis* are 1.9±0.2 cm long (mean±SD, n = 40), 1.4±0.2 cm wide and 2.4±0.6 g (Xiao et al., 2001). Insect larvae infestation is frequent and varies among years: 22.3–56.9 % of *Q. variabilis* seeds were infested in secondary stands during 2001 to 2004 (Xiao et al., 2001, 2007). Due to their high nutritional value (54.17% of crude starch and 17.6 J g⁻¹ of caloric value in kernels) and fragile coat (0.2 mm thick), seeds of *Q. variabilis* are favored by rodents for eating and hoarding (Xiao et al., 2003b; Cheng et al., 2007; Xiao et al., 2007).

Experimental seeds were collected in a primary stand in September 2004. Seed infestation was identified based on observations of openings or black pinpricks on the seed coat. Black pinpricks, left by insects when they lay eggs, are signs of weevil infestation to seeds with larvae concealed inside. When larvae leave seeds, one or two openings are left on the seed coat. The kernels of infested seeds were partly damaged. Sound seeds (SS, 2.8±0.3 g, 2.2±0.2 cm long, 1.4±0.2 cm wide, n = 40, mean±SD) were defined as intact sound seeds without any infestation marks such as openings and black pinpricks on the seed coat. Larvae-emerged seeds (LE, 1.7±0.2 g, 2.1±0.3 cm long, 1.3±0.1 cm wide) contained one or two openings on the seed coat and larvae had emerged. Larvae-concealed seeds (LC, 2.7±0.3 g, 2.2±0.1 cm long, 1.4±0.1 cm wide) contained one or two black pinpricks on the seed coat, a sign of infestation and that larvae were concealed inside. Kernels of LE and LC seeds are partially damaged by infestation. The three categories of seeds are similar in size but SS and LC seeds are heavier than LE seeds.

Seeds were marked following the tin-tagged method: a 0.5 mm diameter hole is drilled at the distal end of each seed and a unique coded tin-tag (3 cm × 1 cm, 0.1g) is tied to each seed using a 3 cm piece of fine steel wire (Zhang and Wang, 2001). The efficiency of this method in tracking seeds dispersed by small rodents has been demonstrated by a number of field and enclosure studies (see Cheng et al., 2005; Xiao et al., 2006; Yi et al., 2008).

1.4 Enclosure design

Four outdoor enclosures (10 m × 10 m) were constructed using bricks in an open field. Enclosure walls were 1.5 m above and 0.3 m below the ground. Each enclosure was covered with plastic cloth to prevent predators or other animals from entering. Grass and shrubs were planted inside the enclosures to simulate natural vegetation and cover (about 20%). A wooden
nest box (40 cm × 18 cm × 18 cm) and a water plate were placed in one corner. A seed station (0.5 m × 0.5 m) was located in the centre of each enclosure (see Cheng et al., 2005; Zhang et al., 2008a; Chang et al., 2009).

1.5 Experimental protocol

Independent and pairwise tests were conducted to test the hoarding responses of *L. edwardsi* to sound (SS) and infested seeds (LE and LC). In the independent test, the three categories of seed were provided to rats separately (three treatments: SS, LC and LE, 20 seeds per rat per treatment). In the pairwise test, sound and infested seeds were provided in pairwise combinations (two treatments; 20 SS + 20 LC; 20 SS + 20 LE, 40 seeds per rat per treatment). Six adult male and six adult female rats were used in each treatment. Sixty animals (12 rats by five treatments) were used in our experiments as we used each animal only once.

One week before testing, animals were fed with *Q. variabilis* seeds in the laboratory for dietary acclimation. Following seed placement a rat was introduced into the enclosure from 1630–1730 h and removed the following morning between 0900–1000 h. All seeds and their fragments were recorded and removed. Rats stayed in the enclosure for one night (16–17 hr). Soil in the enclosures was scarified and new water and nest substrate were provided for new tests.

Seed fates were defined following Cheng et al. (2005) as eaten (E) if seeds were eaten or partially eaten with tag or seed fragments left on the ground surface or in the nest, buried (B) if intact tagged seeds were buried in soil with tin-tag left on ground surface and intact after removal (IR) if intact tagged seeds were found on the ground surface after removal. We defined total removed seeds or R as the sum of the above three fates.

We used seed number and percentage of seed mass of seed fate to evaluate preferences of *L. edwardsi* between sound and infested seeds. Percentage of seed mass was calculated as

\[ P_i = M_i / M \times 100\%
\]

where \( P_i \) is percentage of seed fate \( i \); \( M_i \) is mass of seed fate \( i \); \( i \) denotes E, B, IR and R; \( M \) is mass of total released seeds. Partially eaten or chewed seeds with dental marks were recorded as eaten in number but were recorded as not eaten in seed mass.

1.6 Statistical analyses

SPSS for Windows v13.0 (SPSS Inc., Chicago, USA) was used. An explore test was used to test the data for normality and homogeneity. For both independent and pairwise tests a MANOVA was used to test the effect of infestation on seed preferences of *L. edwardsi*, seed fate (E, B, IR, R) was the dependent variable and seed category (SS, LE, LC) was the fixed factor. Fate of IR was excluded from analysis due to the small sample size.

2 Results

An effect of infestation was found between LE and SS. When LE and SS were provided to rats independently, the number of seeds in each fate (\( F_{3, 20} = 2.878, P = 0.046 \)), but not the percentage of mass (\( P > 0.05 \)) was influenced by infestation. For the number of seeds, more LE seeds were eaten (\( F_{1, 22} = 7.590, P = 0.012 \)) and fewer of them were buried in soil (\( F_{1, 22} = 5.664, P = 0.027 \)) than SS. In terms of percentage of mass, fewer LE seeds were removed from seed stations (\( F_{1, 22} = 7.336, P = 0.014 \)) or buried in soil (\( F_{1, 22} = 5.560, P = 0.029 \)) than SS (Fig. 1A, 1B). When LE and SS were provided to rats simultaneously, seed fate was affected by infestation both in number (\( F_{3, 20} = 4.678, P = 0.014 \)) and percentage of mass (\( F_{3, 20} = 6.204, P = 0.004 \)). Fewer LE seeds were removed from seed stations (R) and buried in soil (B) than SS both in number (R: \( F_{1, 22} = 4.500, P = 0.047 \); B: \( F_{1, 22} = 6.409, P = 0.020 \)) and percentage of mass (R: \( F_{1, 22} = 8.955, P = 0.007 \); B: \( F_{1, 22} = 4.337, P = 0.045 \)). Fewer LE seeds were eaten in percentage of mass than SS (\( F_{1, 22} = 4.549, P = 0.044 \)) (Fig. 1C, 1D). No effects of infestation were found between LC and SS seeds (all \( P > 0.05 \)) (Fig. 2).

3 Discussions

Our results show that *L. edwardsi* hoarded more sound seeds and larva-concealed seeds than larva-emerged seeds. Compared to sound seeds, more larva-emerged seeds were eaten in terms of the number of seeds (no significant difference in pairwise tests), but fewer larva-emerged seeds were eaten in terms of percentage of mass (no significant difference in independent tests). Some LE seeds were rejected after being partially eaten or chewed a mark. These seeds were recorded as eaten seeds when calculating the numbers of seeds (actually they were not eaten) and as not eaten seeds in percentage of mass calculations. Seed mass is more applicable in evaluating the seed eating preferences of focal rats. Therefore, *L. edwardsi* likely ate less larva-emerged seeds than sound seeds. These results agree with the observations that serious infestation may make seeds less attractive to seed-eating animals (Leiva and Fernández-Alés, 2005; Gálvez and Jansen, 2007). Hoarded food items are not a random selection of those items encountered (Vander Wall, 1990). Nutritional quality...
Fig. 1 Responses of *Leopoldamys edwardsi* to sound and larvae-emerged *Quercus variabilis* seeds during an independent test (A, B) and in pairwise tests (C, D)

R = total removed seeds; E = eaten; B = buried; IR = intact after removal; * P < 0.05 and ** P < 0.01; mean±SE.

**is one of the most important factors that affects what to eat or hoard for hoarders. Generally, hoarders consume low-value foods in situ and hoard high-value items to satisfy future nutritional demand (Steele et al., 1996; Dearing et al., 2000; Brewer, 2001; Shimada, 2001; Izhaki, 2002; Xiao et al., 2005; Ganesh and Davida, 2005). For example, Zhang et al. (2008b) showed that small rodents prefer to consume small seeds of Liaodong oak *Quercus liaotungensis* at seed stations and hoard large ones. Another study conducted in the same enclosures also showed that *L. edwardsi* tended to eat small seeds (*Q. serrata* and *Cyclobalanopsis glauca*) and hoard large ones *Q. variabilis* (Chang et al., 2009). Our results agree with such previous studies. In our ex-**
periments, the mass of larvae-emerged seeds was significantly lighter than that of sound seeds and lar-
va-concealed seeds because their kernels were mostly consumed by insect larvae. Kernels of larvae-concealed
seeds were also partially infested, but larvae, as a pro-
tein-rich complement, may compensate for the loss of
nutrition by infestation (Steele et al., 1996; Silvius,
2002). Larvae-emerged seeds generally have lower nu-
tritional value than sound seeds and larvae-concealed
seeds, therefore, sound seeds and larvae-concealed
seeds were preferred for hoarding while larvae-emerged
seeds were mostly rejected after chewing or being par-
tially eaten. Unfortunately, our conclusions are limited
because did not compare larvae-concealed seeds and
larvae-emerged seeds directly.

Our results suggest that larvae-concealed seeds as
well as sound seeds were favored by *L. edwardsi* for
hoarding. This suggestion is supported by previous
work (Stiles and Dobi, 1987; Weckerly et al., 1989;
Dixon et al., 1997). The responses of rodents to seeds
concealing lar valve have been poorly investigated. In
contrast to our findings, Xiao et al. (2003a) conducted a
field study in the same study area as us and showed that
seed-eating rodents tended to consume LC seeds in situ
and hoard sound seeds. This discrepancy was very likely
casted by differences in field observations (Xiao et al.,
2003a) versus enclosure conditions (this study). In the
field, many rodent species including some non-hoarders
(e. g. *R. nitidus* and *N. fulvescens*), may be responsible
for seed consumption. Unlike hoarders who hoard
high-quality foods for future use, non-hoarders tend to
consume high-quality foods immediately. Due to the
high protein bonus from insect larvae, infested seeds
with larvae concealed inside might be more favored by
non-hoarders (Andersen and Folk, 1993; Steele et al.,
1996; Silvius, 2002; but Gálvez and Jansen, 2007).

Our findings suggest that *L. edwardsi* can discrimi-
nate between sound seeds and seeds previously infested
by larvae and are supported by previous researches
(Smel et al., 1996; Xiao et al., 2003a; Oorschot, 2003).
Our results also suggest that *L. edwardsi* cannot distin-
guish larvae-concealed seeds from sound seeds (Semel
and Andersen, 1988; Weckerly et al., 1989; Gálvez and
Jansen, 2007, but see Dixon et al., 1997; Silvius, 2002;
Xiao et al., 2003a). Openings on the seed coat and seed
weight may be important cues used by for *L. edwardsi*
 to discriminate sound and infested seeds. Larvae
emerged seeds often have one or two openings on the
seed coat and are lighter than sound seeds and lar-
va-concealed seeds. In addition, chewing might be
involved in food selection because dental marks were
observed on almost all rejected infested seeds. A similar
phenomenon was observed by Gálvez and Jansen
(2007).

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