Behavioural Processes 85 (2010) 163–166

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Effects of burrow condition and seed handling time on hoarding strategies of Edward's long-tailed rat (*Leopoldamys edwardsi*)

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ARTICLE INFO

Article history:
Received 21 January 2010
Received in revised form 18 June 2010
Accepted 5 July 2010

Keywords:
Edward's long-tailed rats (*Leopoldamys edwardsi*)
Burrow condition
Scatter-hoarding
Larder-hoarding
Handling time

ABSTRACT

Many hoarding rodents use burrows not only for dwelling and protection from natural enemies, but also for food storage. However, little is known how burrows used by scatter-hoarding animals influence their foraging behaviors. In addition, handling time for a given food item has a fundamental impact on hoarding strategies of these hoarding animals: food items with longer handling time are more likely to be hoarded due to increasing predation risk because the animals spend more time outside their burrows if they consumed such food. By providing with two types of artificial burrows (aboveground vs. underground) and two types of food items (i.e. seeds) with contrasting handling times, we investigated how burrow condition and handling time co-influence hoarding strategies of a key scatter-hoarding rodent, Edward's long-tailed rat (*Leopoldamys edwardsi*) in large enclosures in southwest China. We found that only a few animals larder-hoarded fewer seeds when only aboveground burrows were available, while over 80% of the animals preferred to use the underground burrows and hoard significantly more seeds in the burrows when both aboveground and underground burrows were provided simultaneously. We also found that seed handling time significantly affected hoarding strategies of the animals: they consumed and/or scatter-hoarded more *Camellia oleifera* seeds with shorter handling time outside the burrow, but consumed and larder-hoarded more *Lithocarpus harlandii* seeds with longer handling time in underground burrows. Our study indicates that both burrow types and seed handling time have important impacts on hoarding strategies of scatter-hoarding animals.

1. Introduction

Food hoarding is an important adaptive strategy for many animals during periods of food shortage (Smith and Reichman, 1984; Vander Wall, 1990). There are two major types of hoarding strategies: scatter-hoarding and larder-hoarding. Scatter-hoarding means that food is distributed as a large number of small caches with one or several food items over a relatively large area, perhaps throughout the home range of the animal, while larder-hoarding means that a mass of food is stored in a centralized location such as burrows (Vander Wall, 1990; Jenkins and Breck, 1998). Each of the two hoarding strategies has both advantages and disadvantages. Larder-hoarding appears to facilitate the maintenance and defense of the accumulated stores; but for animals unable to defend their stores, it is catastrophic loss that entire supply of cached food will be taken by intraspecific or interspecific competitors (Vander Wall, 1990; Hurly and Lourie, 1997; Vander Wall and Jenkins, 2003). The numerous concealed locations of scatter caches may reduce the risk of pilferage, however, scatter-hoarders have to increase extra expense in predation risk, spatial memory and increased energy use associated with cache recovery (Stapanian and Smith, 1978, 1984; Clarkson et al., 1986; Daly et al., 1990, 1992; Clarke and Kramer, 1994a; Leaver, 2004; Murray et al., 2006). There may be a trade-off between these two hoarding strategies for hoarding animals. Many scatter-hoarding rodents are found to use these two hoarding strategies depending on their sexes, ages and other conditions (Hurly and Robertson, 1990; Clarke and Kramer, 1994b; Barkley and Jacobs, 2007).

Many hoarding rodents use burrows not only for dwelling and protection from natural enemies, but also for food storage. Foraging animals are always exposed to the risk of being victim of other predators (Lima and Dill, 1990; Onuki and Makino, 2005). Especially for scatter hoarders, frequent caching and recovering inevitably prolong time spending outside the burrow. From this point of view, larder-hoarding has an advantage to avoid predation risk by shortening time spending outside the burrow. Storing food in burrows is a typical larder-hoarding behavior, however, burrow hoarding is also risky if the hoarder could not defend it from

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doi:10.1016/j.beproc.2010.07.004

pilferage and the loss of entire storing food is fatal for hoarders (Vander Wall, 1990; Vander Wall and Jenkins, 2003). So, the security of burrow is very important for larder-hoarders and covert and secure burrow can increase the fitness of larder-hoarding. However, little is known how burrows used by scatter-hoarding animals influence their foraging behaviors. Hurly and Robertson (1990) suggested that the availability of middens (i.e. burrow) can influence hoarding patterns of red squirrels (*Tamiaseiurus hudsonicus*): they larder-hoarded more cones when well established middens were provided.

For a given food item (i.e. seed), handling time (correlated with seed size and hull hardness/thickness) is another major factor influencing behavioral decisions of hoarding rodents (Jacobs, 1992; Hadj-Chikh et al., 1996; Xiao et al., 2003, 2006a). During foraging process, animals should minimize the time to handle food since longer handling time means higher predation risk. For example, Jacobs (1992) found that grey squirrels (*Sciurus carolinensis*) hoarded more food with longer handling time over that with shorter handling time, indicating that this strategy could maximize both foraging and hoarding efficiency. However, it is also poorly understood whether food handling time has some effects on burrow use by scatter-hoarding animals, including their hoarding behaviors.

By providing with two types of artificial burrows (aboveground vs. underground) and two types of food items (i.e. seeds) with contrasting handling time, we investigated how burrow condition and seed handling time co-influence hoarding strategies of a key scatter-hoarding rodent, Edward's long-tailed rats in large enclosures in southwest China. We tested the following two hypotheses: (1) hoarding animals would prefer to use the more safe underground burrows over the aboveground ones and thus they also larder-hoard more seeds in underground burrows when these two burrow types are available and (2) animals consumed and/or scatter-hoarded more seeds with shorter handling time outside the burrow, but consumed and larder-hoarded more seeds with longer handling time in underground burrows based on the handling time hypothesis.

2. Materials and methods

2.1. Study site and subjects

The study was conducted in a Banruosi Experimental Forest (altitude 700–1000 m, 31°4′N, 103°43′E) in the Dujiangyan Region, Sichuan Province, southwest China. The vegetation is subtropical evergreen broadleaved forest, where nut-bearing species are most common. Two common seed species, *Camellia oleifera* and *Lithocarpus harlandii* and one key scatter-hoarding rodent, Edward's long-tailed rats were used in this study because these two seed species are preferentially hoarded by Edward's long-tailed rats (Xiao et al., 2003, 2004, 2005, 2006a; Xiao and Zhang, 2006c; Cheng et al., 2005). Though they vary greatly in seed size, nutrients and hull hardness, here we focused primarily on handling time (proportional to seed size and hull hardness) between these two seed species: Edward's long-tailed rats spend 771.78 ± 200.34 s consuming one *L. harlandii* seed but only 53.06 ± 31.4 s for one *C. oleifera* seed (Table 1, see Xiao et al., 2003).

In the study site, Edward's long-tailed rats are large nocturnal rodents (200–500 g adult mass) with high densities. Our previous and ongoing studies have shown that Edward's long-tailed rats are principal scatter-hoarders for many large-seeded plants including the two seed species used in this study (Xiao et al., 2003, 2008; Cheng et al., 2005; Chang et al., 2009). To trap the animals we used large wired cage traps (30 cm × 25 cm × 20 cm, of our own design approved by the Institute of Zoology, CAS) baited with peanuts and small pieces of cabbage as food and water and provisioned with local dry leaves as nest materials. The traps and nest materials protect animals from cold weather and predators. Traps were deployed at 19:00–19:30 and checked after 12 h (dense vegetation and steep landscape on the study site precluded us from checking traps during the night). When checked that time, all captured animals were healthy. The animals in reproductive conditions were released immediately on site. Before experiments, all animals were kept individually in a large mouse cage (50 cm × 30 cm × 25 cm) with adequate laboratory chow, water and nest structures. The room temperature was 10–15 °C and natural photoperiod was at 12:12 h light:dark cycle. During the experiments, adequate water and nest structures were also provided. We trapped nine individuals of Edward's long-tailed rats (four males and five females) in 2006, and eight individuals (three males and five females) in 2007. After experiments (up to 2–3 months), all animals were released where they were captured.

Table 1
Seed characteristics of *Camellia oleifera* and *Lithocarpus harlandii*.

Descriptions	*Camellia oleifera*	*Lithocarpus harlandii*
Seed mass (g)[a]	0.87 ± 0.07	4.56 ± 0.12
Hull thickness (mm)[a]	0.39 ± 0.01	1.45 ± 0.04
Handling time (s)[b]	53.06 ± 31.4	771.78 ± 200.34
Crude fat (% of dry nutmeat)[c]	51.79	0.91
Crude protein (% of dry nutmeat)[c]	10.91	5.80
Crude starch (% of dry nutmeat)[c]	11.74	37.66
Tannin (% of dry nutmeat)[c]	0.10	1.34
J value (per gram of dry nutmeat)[c]	29.56	17.11

[a] Mean ± 1 S.E., $N = 30$.
[b] Handling time means the time that the animal spends consuming one seed (mean ± 1 S.D. Xiao et al., 2003).
[c] From Xiao et al. (2003).

2.2. Burrow design

All experiments were conducted in four large enclosures (10 m × 10 m, see Cheng et al., 2005 for details). In this study, two types of artificial burrows (18 cm × 18 cm × 40 cm) were used in each enclosure: one was aboveground burrow established on the ground at one corner, and the other was underground burrow set at the opposite corner. For underground burrows, PVC pipe (6 cm diameter, 40 cm long) was used to allow the animals to enter or leave the burrow freely. We added enough dry straws as nest materials in each burrow and used a cover to close the underground burrow when necessary. In the center of each enclosure, we set a food station to place seeds and water.

2.3. Experimental procedure

We set four treatments to test the effects of burrow types and seed handling time on hoarding strategies of Edward's long-tailed rats. In Treatments I and II, we only opened the aboveground burrows but closed the underground ones and presented either *C. oleifera* or *L. harlandii* seeds, respectively; while in Treatments III and IV, we simultaneously opened aboveground and underground burrows and presented either *C. oleifera* or *L. harlandii* seeds, respectively. Total 12 individuals had experienced the 4 treatments completely (other individuals data were excluded because they did not complete the whole four treatments).

Before the experiments, each animal was introduced into the enclosure and allowed to move freely for one night. The animal was then tested for a one-night trial and each trial lasted ca. 14 h from 17:30 to 07:30. We labeled seeds with small coded plastic-tags (see Xiao et al., 2006b for details). On the first day we presented each animal with 50 *C. oleifera* or *L. harlandii* seeds. In the morning of the second day, we searched all released seeds or their fragments

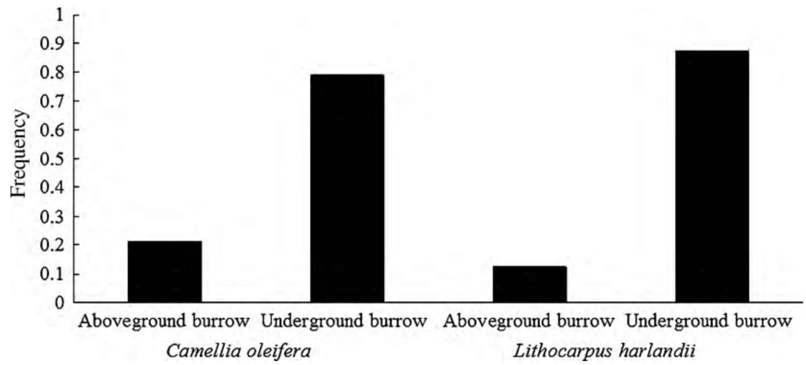

Fig. 1. Frequency to aboveground or underground burrows selected by Edward's long-tailed rats using seeds of either *Camellia oleifera* or *Lithocarpus harlandii* ($N = 12$).

and recorded their fates (e.g. eaten outside the burrow, eaten in the burrow, scatter-hoarded and larder-hoarded), then we removed all seeds and continued the next trial. Eaten seeds were divided into those outside the burrow (EOB) and in the burrow (EIB); scatter-hoarded seeds (SH) were those buried intact in the surface soil; and larder-hoarded seeds (LH) were those stored intact in the burrow. Seeds that were removed from the station but left intact on the ground were not included in the analysis.

2.4. Statistical analysis

Fisher's Exact Test was used to test the frequency of two burrow types selected by animals. We used the proportion data of eaten seeds, scatter-hoarded seeds and larder-hoarded seeds. Before analysis, the proportion data were arcsine-square-root transformed. A repeated-measures two-way ANOVA was used to test the difference in the proportion of seeds either eaten, scatter-hoarded or larder-hoarded with seed type and burrow type as fixed factors and one-night trial for each individual as a random factor.

3. Results

In Treatments III and IV, the animals preferred to use the underground burrows over the aboveground ones regardless of providing either *C. oleifera* seeds (Fisher's Exact Test, $p = 0.008$) or *L. harlandii* ones (Fisher's Exact Test, $p < 0.001$) seeds (Fig. 1).

The animals ate more *C. oleifera* seeds than *L. harlandii* ones outside the burrow with or without underground burrows ($F = 55.027$, $df_1 = 1$, $df_2 = 11$, $p < 0.01$). Burrow treatment had significant effect on the amount eaten outside the nest ($F = 7.441$, $df_1 = 1$, $df_2 = 11$, $p = 0.020$), and its interaction with seed type also had a significant effect with more *L. harlandii* seeds eaten when only aboveground burrow was available compared with when two burrow types were provided ($F = 16.158$, $df_1 = 1$, $df_2 = 11$, $p = 0.002$). More *L. harlandii* seeds were eaten in the burrow than *C. oleifera* ones ($F = 17.101$, $df_1 = 1$, $df_2 = 11$, $p = 0.002$), and burrow treatment also had significant effects on whether *L. harlandii* or *C. oleifera* seeds were eaten in the burrow or not ($F = 5.778$, $df_1 = 1$, $df_2 = 11$, $p = 0.035$) (Fig. 2).

Although the animals scatter-hoarded more *L. harlandii* seeds outside the burrow when two burrow types were provided, the amount scatter-hoarded was not significant between both the two seed types ($F = 2.338$, $df_1 = 1$, $df_2 = 11$, $p = 0.154$) and burrow treatment ($F = 0.956$, $df_1 = 1$, $df_2 = 11$, $p = 0.349$), including their interaction ($F = 1.455$, $df_1 = 1$, $df_2 = 11$, $p = 0.253$). More *L. harlandii* seeds were hoarded in the burrow than *C. oleifera* ones ($F = 25.340$, $df_1 = 1$, $df_2 = 11$, $p = 0.001$), and both seed type had more seeds hoarded in the burrow when two burrow types were provided ($F = 9.322$, $df_1 = 1$, $df_2 = 11$, $p = 0.011$). There was a significant effect on larder-hoarding from the interaction between seed type and burrow treatment ($F = 12.175$, $df_1 = 1$, $df_2 = 11$, $p = 0.005$) (Fig. 2).

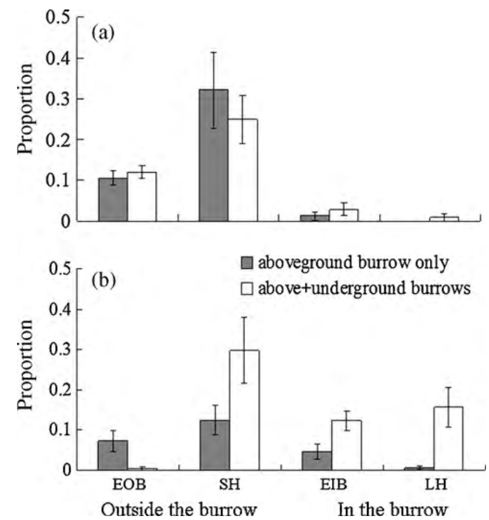

Fig. 2. Eating and hoarding strategies (mean ± 1 S.E.) to seeds of *Camellia oleifera* (a) and *Lithocarpus harlandii* (b) by Edward's long-tailed rats (EOB = eaten outside the burrow, SH = scatter-hoarded, EIB = eaten in the burrow, LH = larder-hoarded).

4. Discussion

In this study, our results support our prediction that scatter-hoarding Edward's long-tailed rats preferred to use underground burrow for dwelling and food storage when both aboveground and underground burrows were provided. When only the aboveground burrows were available, the animals consumed more seeds outside the burrow and only a few animals hoarded few seeds in the burrow. However, over 80% of the animals used the underground burrows and hoard significantly more seeds in the burrow when both aboveground and underground burrows were provided simultaneously.

On the one hand, predation risk has significant impacts on foraging behavior of granivorous rodents and they adopt various strategies to avoid predation hazard during foraging, such as a short excursion (Longland and Price, 1991), rapid transportation between patches (Newman et al., 1988), decreasing food handling time outside the burrow (Sone, 2004), increasing food-carrying time (Onuki and Makino, 2005) and storing food in a safe area (Fleming and Brown, 1975; Hurly and Robertson, 1990). These results suggest that foraging (i.e. eating and/or hoarding) outside the burrow is more dangerous in the field. From this view of predation risk, covert and secure underground burrows are fitter for larder-hoarding than exposed and unsafe aboveground ones. On the other hand, the physical characteristics of burrow, such as seasonal fluctuations in temperature and humidity, could provide some of the selective pressures for burrow hoarding behavior (Fleming and Brown, 1975). Empirical and experimental observations indicate that temperature fluctuations within burrow decreases with increasing burrow depth and that relative humidity within burrow is always high (Studier and Baca, 1968; Fleming and Brown, 1975). Because burrow usually provides a cooler, more stable temperature regime and high relative humidity, it can serve as storage area for food caches and as retreats from predators. So, compared with aboveground burrows, underground ones have more advantages for larder-hoarding.

In addition, we also found that seed handling time had important effect on burrow use and hoarding strategies of Edward's long-tailed rats. The animals spend ca. 1 min consuming one *C. oleifera* seed, resulting in more seeds eaten outside the burrow. However, *L. harlandii* seeds are large with hard hull and thus significantly increase handling time when they are consumed by animals. We found that more *L. harlandii* seeds were either consumed or hoarded in the burrow especially when both aboveground and underground burrows are provided. In contrast, more *C. oleifera* seeds were eaten outside the burrow or scatter-hoarded with or without underground burrows. This supports the handling time hypothesis that animals can adaptively adjust their eating and hoarding strategies according to different seed handling time. Instant consumption outside the burrow may incur an increased predation risk due to a longer handling time (Jacobs, 1992; Xiao et al., 2003). For example, Xiao et al. (2006a) conducted field experiments in the same study site and found that small *Castanopsis fargesii* seeds were eaten immediately in the seed station, while more seeds with a hard hull (e.g. *L. harlandii*) were removed from the source. Lu and Zhang (2005a,b) found that both white-bellied rats (*Niviventer confucianus*) and large field mouse (*Apodemus peninsulae*) preferred to eat seeds of *Quercus liaotungensis* with a soft hull *in situ* but remove and hoard seeds of *Prunus armeniaca* with a very hard hull in enclosure experiments.

In conclusion, our study suggest that both burrow condition and seed handling time had important effect on hoarding strategies of Edward's long-tailed rats. We found that Edward's long-tailed rats preferred to use underground burrows over aboveground ones for dwelling and food storage, which can reduce predation risk. We also found that the animals consumed and/or scatter-hoarded more *C. oleifera* seeds with shorter handling time outside the burrow, but consumed and larder-hoarded more *L. harlandii* seeds with longer handling time in underground burrows.

Acknowledgements

We thank the Subalpine Mountain Plant Garden of West-China, CAS, and the Forest Bureau of Dujiangyan City of Sichuan Province, for support. Field assistance is provided by Mingmin Jiang and Xu Gao. We are very grateful to the editor and to the two anonymous reviewers for their critical comments and constructive suggestions for revising and improving the manuscript. Funds were provided by National Natural Science Foundation of China and the Knowledge Innovation Program of Chinese Academy of Sciences. The experiments comply with the current laws of the country in which they were performed.

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