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Comparison of food hoarding of two sympatric rodent species under interspecific competition

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ABSTRACT

Competition can greatly affect the food hoarding strategies of rodents and the fate of seeds hoarded. In order to understand the influence of interspecific competition on food caching behavior of sympatric rodents, we investigated food hoarding patterns of two sympatric rodent species, buff-breasted rat (*Rattus flavipectus*) and Chinese white-bellied rat (*Niviventor confucianus*), and compared their responses and adjustment in hoarding behavior under interspecific competition. The results showed that: (1) the buff-breasted rat larder hoarded seeds only, while Chinese white-bellied rat hoarded seeds in both larder and scatter forms; (2) two species of rodents both larder hoarded more seeds when competitors were present; and (3) the Chinese white-bellied rats adjusted their seed hoarding from scatter to larder when competitors were introduced, which reduced the seed availability. Therefore, we concluded that rodents would adjust their food hoarding strategy when interspecific competitors were present, and this may produce a different effect on the fate of seeds and the recruitment of plants.

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1. Introduction

Food hoarding is a food storage behavior of some rodents, important for their survival during the period when the food is scarce (Smith and Reichman, 1984; Vander Wall, 1990; Li and Zhang, 2003; Carlo et al., 2011). Rodent species with different morphological and behavioral characteristics usually exhibit a different food hoarding strategy (Price et al., 2000; Cheng et al., 2005; Lu and Zhang, 2008; Chang and Zhang, 2011). Hoarders which are strong enough to defend cached food items will larder hoard their food. Otherwise, food may be scatter-hoarded (Vander Wall and Jenkins, 2003; Lu and Zhang, 2008). Furthermore, competitions from inter- and intra-specific individuals can influence the hoarders selection of storing patterns (Hopewell et al., 2008; Tong et al., 2012). Under the presence of competitors, food hoarders usually adopt various measures to reduce pilferage of competitors to their stored-food (Vander Wall and Jenkins, 2003; Dally et al., 2006; Hopewell et al., 2008; Tong et al., 2012). The strategies of cache protection adopted by food hoarders include: (1) storing more food to offset loss from stealing (Dally et al., 2006; Male and Smulders, 2007); (2) reducing the amount of food stored (Stone and Baker, 1989; Lahti and RytkÖnen, 1996; Brotons, 2000; Dally et al., 2005); (3) transporting food further away from food sources (Stapanian and Smith, 1984; Clarkson et al., 1986; Dally et al., 1992; Vander Wall, 1995; Leaver et al., 2007); (4) delaying hoarding food until there are no competitors in the vicinity (Bugnyar and Kotrschal, 2002); and (5) changing from scatter hoarding to larder hoarding (Jenkins et al., 1995; Preston and Jacobs, 2001).

It was well documented that seed dispersal is a critically important phase in the life cycle of plants, and the dispersers including rodents usually play a crucial role during this course (Wang and Smith, 2002; Forget et al., 2005; Zhang et al., 2005; Heleno et al., 2011). However, the effectiveness of seed dispersal by seed-caching animals is still contentious (Vander Wall, 1990; Gómez et al., 2008). When dispersing large quantity of seeds, these hoarding animals also consume a big proportion of these seeds (Schupp, 1990; Mendoza and Dirzo, 2007). Consequently, the fate of seeds is closely correlated with rodents' food hoarding strategies, such as larder hoarding and scatter hoarding (Smith and Reichman, 1984; Vander Wall, 1990; Jenkins and Breck, 1998; Lu and Zhang, 2008). Larder hoarding refers to an animal's behavior of storing seeds in a single place where it is unfavorable for seedling establishment. Scatter hoarders store seeds in certain sites which may provide the necessary microclimate condition for germination. Also, scatter-hoarded seeds of escaping from predation are more likely to establish seedlings (Price and Jenkins, 1986; Vander Wall, 1990, 2001; Zhang et al., 2005).

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Influences of competition on animal food hoarding behavior may depend on the way how competitors behave (*e.g.* the way in which competitors pilfer stored food) (Preston and Jacobs, 2001; Vander Wall and Jenkins, 2003; Leaver, 2004), or competitors may affect hoarders behavior by their presence or invisible clues (*e.g.* odor, sound) (Giraldeau et al., 1994; Hopewell, 2008; Stulp et al., 2009; Tong et al., 2012; Zhang et al., 2011). In this study, by introducing an interspecific competitor into the enclosure containing a resident (either a buff-breasted rat or a Chinese white-bellied rat), we investigated: (1) the influence of competition on rodents food hoarding behavior; (2) how hoarders adjusted hoarding patterns between scatter and larder when interspecific competition was introduced; and (3) the influence of interspecific competition on the fate of seeds stored by rodents. We predicted that introducing an interspecific competitor would greatly alter the process of food hoarding and the hoarding strategy of the resident rodent.

2. Materials and methods

2.1. Study area and experimental animals

We conducted this study in the tropical rain forest in the Xishuangbanna region (21°09′–22°36′N, 99°58′–101°50′E) of Yunnan Province, Southwestern China. The study site was located in the upper reaches of Lancang (Mecong) river, near the southern part of Mt. Hengduan, with an altitude between 475 m and 2430 m. This area has a subtropical climate, influenced by Indian monsoons in the summer and continental air masses in the winter. See detailed information given by Tong et al. (2012).

Buff-breasted rats (*Rattus flavipectus*) and Chinese white-bellied rats (*Niviventor confucianus*) were live trapped using steel-wire live traps (12 cm × 12 cm × 25 cm) from January to March 2009. Healthy adult individuals were taken to the laboratory using live traps, except for pregnant and lactating females which were released immediately on-site. All animals used were numbered, weighed, sexed, and housed individually in different rooms using PVC cages (37 cm × 26 cm × 17 cm). These animals were raised under natural photoperiod and ambient temperature within 18–25 °C. Dry leaves and cotton were provided as nesting material. Experimental subjects were fed for at least one week with fresh water and food before being used for tests. After this study, experimental animals were either retained for other studies or released. The research protocol was approved by the Ethics Committee of Zhengzhou University and experimental protocol was in accordance with guidelines outlined in the China Practice for the Care and Use of Laboratory Animals.

2.2. Enclosure design

Our tests were conducted from February to March 2009 in four 10 m × 10 m semi-natural enclosures constructed in an artificial forest (mainly rubber trees). The enclosures were 1.5 m high. They were extended 20 cm below ground level and covered with wire mesh on top to prevent rodents from escaping and other animals entering. The habitats in the enclosures were similar to the site where the animals were sourced. They consist of a variety of shrubs and herbaceous plants. A wire nest box (40 cm × 30 cm × 20 cm) and a water bowl were placed in one corner of each enclosure. A wooden seed station was provided, placed in the center of each enclosure, containing the seeds of *Lithocarpus truncates* (Fagaceae) (Lu and Zhang, 2005, 2008; Zhang and Zhang, 2007).

2.3. Experimental protocol

During the experiment, each animal was kept continuously in an enclosure for a 3× 24 h period. The first 24 h phase was used for habituation, when fresh water and 40 marked *L. truncatus* seeds were provided. The second 24 h was assigned for control treatment. The third 24 h was the treatment period to determine the effect of interspecific competition. During this period, an animal competitor was placed in a steel-wire cage (12 cm × 12 cm × 25 cm) with food, in the opposite corner to the nest box of the focal animal. After every 24 h period, we removed all seeds and their fragments, cleaned up the nest box, recorded the fate of seeds and refreshed the water. We then supplied 40 new marked *L. truncatus* seeds. Twelve buff-breasted rats (♀/♂: 6/6; body weight 151.28 ± 4.28 g, mean ± SE) and twelve Chinese white-bellied rats (♀/♂: 6/6; body weight 69.75 ± 9.86 g, mean ± SE) were used as experimental subject in this research, and the both were used as competitors for each other.

The fate of seeds were checked and recorded following the methods used by Lu and Zhang (2005) and Xiao et al. (2006): (i) eaten *in situ* (EI): the kernel was eaten at or near the seed station; (ii) eaten after removal (ER): the kernel was eaten after removal from the station. The tag or seed fragments remained on the ground surface; (iii) scatter-hoarding (SH): the tagged seeds were buried in the soil and intact; (iv) larder-hoarding (LH): the tagged seeds were transported into nest box and intact; (v) abandoned on the surface (AS): the tagged seeds were abandoned on the surface of the ground after removal and intact; and (vi) intact *in situ* (IS): the tagged seeds were not moved from the station and intact.

2.4. Seed collection and marking

L. truncatus is widely distributed in our study area and the seeds of this plant (1.19 ± 0.31 g, mean ± SE, n = 50 in fresh weight) have a woody, hard hull. We collected seeds during the fruiting period. The intact seeds were chosen and marked following Zhang and Wang (2001). A tiny hole was drilled into the edge of the seed endocarp and a unique coded plastic tag (3 cm long and 2 cm wide) was tied on the seed with a 10 cm long fine steel wire. This method has been widely employed in tracking fate of dispersed seeds in previous studies, both in the field and within enclosures (Lu and Zhang, 2004; Xiao et al., 2006; Gómez et al., 2008).

2.5. Data analysis

All statistical analysis was carried out using SPSS for Windows (Version 13.0). Wilcoxon Test was used to analyze the effect of interspecific competition on the food hoarding behavior of buff-breasted rat and Chinese white-bellied rat. The data from male and female were pooled because no significant differences were found within these groups.

3. Results

3.1. Food hoarding strategy of buff-breasted rat and Chinese white-bellied rat

On average, 12.7 ± 10.5 (mean ± SE) seeds were moved into their nests by buff-breasted rats. Only 0.5 ± 0.8 seeds were consumed *in situ*, 0.4 ± 0.7 seeds were eaten after removal and 0.8 ± 1.3 seeds were left on the ground surface. No seeds were buried by buff-breasted rats. They stored food in the form of larder hoarding (Fig. 1). Chinese white-bellied rats moved 10.8 ± 9.1 seeds into their nest, consumed 0.2 ± 0.4 seeds *in situ*, consumed 0.8 ± 1.2 seeds after removal and left 1.2 ± 0.4 seeds on the ground surface. Averages of 0.4 ± 0.9 seeds were buried. Chinese white-bellied rats exhibited both larder and scatter hoarding (Fig. 1).

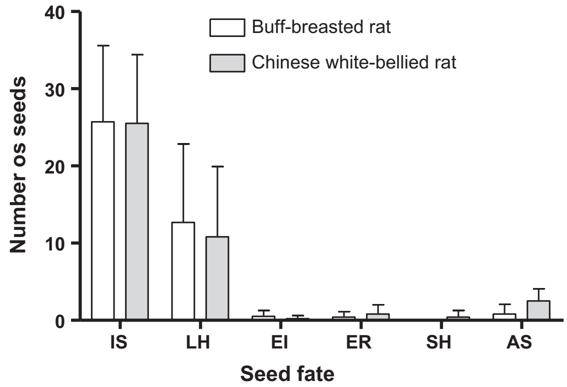

Fig. 1. Hoarding patterns of the buff-breasted rat and the Chinese white-bellied rat on seeds of *L. truncates*. IS: intaction *in situ*; LH: Larder-hoarding; EI: eaten *in situ*; ER: eaten after removal; SH: scatter-hoarding; AS: abandoned on the surface.

3.2. Adjustment in food hoarding patterns under interspecific competition

Buff-breasted rats did not bury any seeds in the presence or absence of interspecific competitors (Fig. 2b). However, these rodents moved a larger number of seeds (192) into the nest for larder hoarding with a competitor present than when the competitor was absent (152), but the difference was not statistically significant ($Z = -0.890$, $P = 0.373$) (Fig. 2a). In presence of an interspecific competitor, the Chinese white-bellied rat larder hoarded remarkably more seeds (204) than without the presence of an interspecific competitor (129) ($Z = -2.362$, $P = 0.018$) (Fig. 2a). They also exhibited scatter hoarding behavior, caching 5 seeds in absence of competitor and 2 when the competitor was introduced ($Z = -0.707$, $P = 0.480$) (Fig. 2b).

3.3. The influence of interspecific competition on seed fate

There is no significant difference in the number of seeds moved by the buff-breasted rat and the Chinese white-bellied rat when the interspecific competitor was present compared to when the competitor was absent (Table 1) (buff-breasted rat: $Z = -1.139$, $P = 0.255$; Chinese white-bellied rat: $Z = -1.572$, $P = 0.116$). The number of seeds under each category of fate, *i.e.* EI, ER and AS, were not significantly influenced by interspecific competitions (buff-breasted rat – EI: $Z = -0.378$, $P = 0.705$; ER: $Z = -1.186$, $P = 0.236$; AS: $Z = -0.638$, $P = 0.524$; Chinese white-bellied rat – EI: $Z = -0.577$, $P = 0.564$; ER: $Z = -1.604$, $P = 0.109$; AS: $Z = -1.709$, $P = 0.088$).

4. Discussion

Rodents have multiple effects on the fate of plant seeds *via* their dispersing and hoarding of seeds, and several factors may affect the interaction between rodents and seeds (Vander Wall, 1990). The results from this current study broaden our understanding of the food hoarding of rodents and its influence on seed fate.

4.1. Food hoarding patterns of the buff-breast rat and Chinese white-bellied rat

The result from this study showed that buff-breasted rat larder hoarded seeds, which confirmed the findings of Tong et al. (2012). We found that Chinese white-bellied rats hoarded seeds in both larder and scatter forms. This was in accordance with previous research results which demonstrated that Chinese white-bellied rats scatter hoarded and larder hoarded seeds in the tropical rainforest and subtropical forest of southern China (Chang and Zhang, 2011; Cao et al., 2011). However, in the dry temperate forest of northern China, this rodent species only larder hoards food (Lu and Zhang, 2008; Zhang et al., 2011). The possible reasons for such difference in food hoarding patterns include the differentiation of climate zone, different competitive environments (Murray et al., 2006), seasonal changes (White and Geluso, 2012), or variation in plant species and community between tropical (our research) and temperate forests (Lu and Zhang, 2008; Zhang et al., 2011). Our results suggest that, during the spring season in a tropical forest, buff-breasted rats are primarily seed consumers; while Chinese white-bellied rats do consume large quantities of seeds, they may play a role in plant seed survival *via* scatter hoarding behavior.

4.2. The response of rodents to interspecific competition

Interspecific interactions of rodents include indirect resource competition (Case and Gilpin, 1974) and direct interference (Schoener, 1983), which can be influenced by various factors, such as season, availability of food resources, breeding state and a variety of other things (Eccard et al., 2011). When rodents utilize a 'larder defense' or 'forage competition' strategy to protect their caches, they tend to hoard more food in front of their competitors (Vander Wall and Jenkins, 2003). In the presence of a competitor, both rodents transferred more seeds into their nest boxes (larder hoarding), indicating they were competing for food. This result provided supporting evidence for defense hypotheses (larder hoarders prevented pilferage through aggressive defense) and forage competition hypotheses (hoarders competed for food and enhanced food hoarding activity) (Vander Wall and Jenkins, 2003; Zhang et al., 2011).

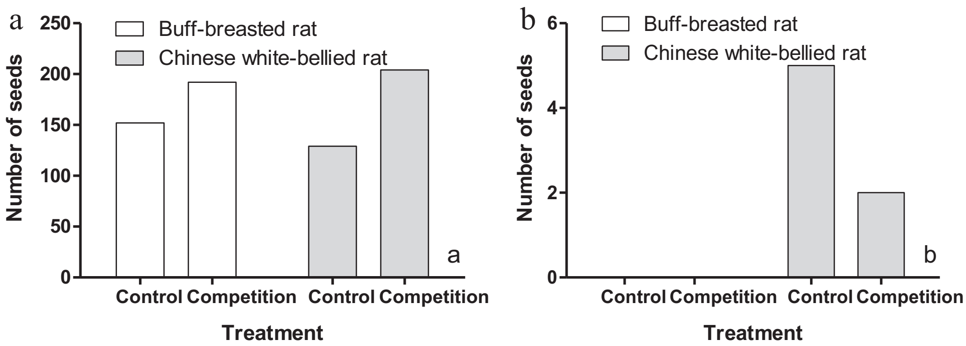

Fig. 2. Seed hoarding patterns of the buff-breasted rat and the Chinese white-bellied rat under conditions with and without interspecific competitors (a: Larder hoarding; b: Scatter hoarding).

Table 1
Seeds fate of *L. truncatus* handled by the buff-breasted rat and Chinese white-bellied rat under condition of interspecific competition.

Species	Treatment	Seed fate					
		IS	LH	EI	ER	SH	AS
R. flavipectus	Control	25.7 ± 9.9	12.7 ± 10.5	0.5 ± 0.8	0.4 ± 0.7	0	0.8 ± 1.3
	Tested	21.8 ± 10.7	16.0 ± 10.5	0.4 ± 0.7	0.9 ± 1.8	0	1.1 ± 1.4
N. confucianus	Control	25.5 ± 8.9	10.8 ± 9.1	0.2 ± 0.4	0.8 ± 1.2	0.4 ± 0.9	1.2 ± 0.4
	Tested	21.5 ± 8.8	17.0 ± 9.4	0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.4	1.0 ± 1.4

Note: IS: intact *in situ*; LH: Larder-hoarding; EI: eaten *in situ*; ER: eaten after removal; SH: scatter-hoarding; AS: abandoned on the surface.

Several previous studies indicated that rodents would adjust food hoarding strategies from scatter to larder after their caches were pilfered by other animals (Clarke and Kramer, 1994; Jenkins et al., 1995; Preston and Jacobs, 2001; Dally et al., 2006). Other studies demonstrated that with pilferage, most rodents did not increase larder hoarding caches but instead increased scatter hoarding (Murray et al., 2006; Huang et al., 2011). The food hoarding behavior of rodents may be affected when conspecific or interspecific individuals are within the line of sight (Leaver et al., 2007; Tong et al., 2012). Korean field mice (*Apodemus peninsulae*) changed their hoarding behavior from scatter to larder when conspecific individuals were present (Zhang et al., 2011). Our results revealed that Chinese white-bellied rats strengthened larder hoarding rather than scatter hoarding, with the presence of interspecific competitors, which supports the larder defense hypotheses (Reichman et al., 1986; Henry, 1986; Dally et al., 1992; Vander Wall et al., 2005), rather than the catastrophic avoidance hypotheses (hoarders changed their foraging and caching strategies in front of competitors) (MacDonald, 1976; Henry, 1986; Leaver et al., 2007). Nonetheless, this result should be considered carefully before applying this conclusion to Chinese white-bellied rats in other regions, because, in previous studies, this rodent species exhibited no scatter hoarding behavior (Lu and Zhang, 2008; Zhang et al., 2011) in temperate areas and weak scatter hoarding in subtropical areas (Chang and Zhang, 2011).

Food hoarding behavior can be enhanced by either pilferage on stored food (Vander Wall and Jenkins, 2003; Dally et al., 2006; Huang et al., 2011) or on the visible presence of a competitor (Tong et al., 2012; Zhang et al., 2011). Note that mechanism behind adjustment between scatter hoarding and larder hoarding under competitive conditions is still unknown and it is worthy of further investigation.

4.3. Linking seed fate to dispersal patterns

Under field conditions, post-dispersal seed fates were determined at large extent by demography, spatial distribution and coexistence of plant species (Janzen, 1971; Hubbell, 1980; Hulme, 1998). The scatter-dispersed seeds had higher survival rate than those larder-dispersed seeds (Russo, 2005), and the seed deposition and dispersal patterns are vital to the eventual seeds fate (Russo, 2005; Wang et al., 2004). Our result revealed that the presence of interspecific individuals resulted in the enhancement of food hoarding behavior, especially larder hoarding (in the nest), and this may result in more seeds being consumed, causing a failure in seedling establishment.

5. Conclusions

(1) The food hoarding patterns of same rodent species may differ in different geographic regions, micro-climate, or different seasons; (2) When the interspecific competitors were present, the Chinese white-bellied rats adjusted their seed hoarding strategy from scatter form to larder; (3) The hoarders enhanced their food hoarding behavior, especially larder hoarding (meaning more seeds were consumed possibly), when interspecific individuals were present. This may result in the reduction of seed survival and seedling establishment.

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