



Scatter-hoarding rodents are better pilferers than larder-hoarders

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ARTICLE INFO

Article history:

Received 23 January 2018

Initial acceptance 15 March 2018

Final acceptance 20 April 2018

MS. number 18-00058

Keywords:

cache pilferage
hoarding behaviour
larder hoarding
reciprocal pilferage
scatter hoarding
seed dispersal

Food hoarding is critical to rodents for their survival and reproduction. However, the seeds cached by rodents often suffer heavy pilferage by competitors. Therefore, compensation for cache loss is crucial, especially for scatter-hoarding rodents, as they cannot aggressively defend their stored seeds, whereas larder-hoarding rodents can. Pilfering caches of other individuals may be an effective way to compensate for cache loss for rodents. Hence, cache pilfering is likely to be as important as hoarding to food-hoarding rodents. Scatter-hoarding rodents may rely on their olfactory abilities and explore a wide area to retrieve their cached seeds, which may help to increase the probability of encountering and pilfering others' caches, whereas it is not essential for larder-hoarding rodents. We hypothesized that rodents that showed stronger scatter-hoarding behaviour would be better pilferers. To test this hypothesis, we investigated the relationship between scatter-hoarding and pilferage behaviours among four coexisting species of rodents using seminatural enclosure experiments in southwest China. Both hoarding and cache pilfering differed significantly between the four species. The predominant scatter-hoarding rodents, red spiny rats, *Maxomys surifer*, had a strong cache-pilfering behaviour, whereas yellow-bellied rats, *Rattus flavipectus*, mainly adopted larder-hoarding strategies and had a weak cache-pilfering behaviour. Chinese white-bellied rats, *Niviventer confucianus*, and chestnut rats, *Niviventer fulvescens*, had moderate scatter-hoarding and cache-pilfering behaviours. The intensity of cache pilfering was negatively correlated with the intensity of larder hoarding, but positively correlated with the intensity of scatter hoarding among the coexisting food-hoarding rodents. Our study suggests that the positive correlation between the intensities of scatter hoarding and cache pilfering is likely to facilitate reciprocal pilferage among scatter-hoarding rodents, which helps to maintain the stability of scatter-hoarding behaviour in these populations.

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Food hoarding is critical to rodents both to survive periods of food shortage and to reproduce (Vander Wall, 1990). Stored food, however, often suffers heavy pilferage due to both interspecific and intraspecific competition (Clarke & Kramer, 1994; Dally, Clayton, & Emery, 2006; Jansen et al., 2012; Lichti, Steele, & Swihart, 2017; Vander Wall et al., 2006). Existing theory of hoarding behaviour predicts that hoarding would not be a stable strategy if the hoarder is not the most likely individual to retrieve the stored foods (Stapanian & Smith, 1978, 1984). However, some studies have found that food-hoarding rodents have evolved a series of strategies to reduce cache pilferage, for example to repeatedly recover and move

caches, aggressively defend caches, switch from scatter to larder hoarding (see review by Dally et al., 2006) or directly disperse seeds to areas with low seed density (Geng, Wang, & Cao, 2017; Hirsch, Kays, Pereira, & Jansen, 2012; Munoz & Bonal, 2011) or open areas (Steele et al., 2014, 2015). Relying on these strategies, cache owners can retrieve most of their stored seeds, although many caches are lost by pilfering (Gu, Zhao, & Zhang, 2017). In addition, some rodents appear to compensate for their cache losses by pilfering food reserves of other individuals, which makes pilferage reciprocal among these rodents (Dittel, Perea, & Vander Wall, 2017; Vander Wall & Jenkins, 2003). Therefore, strategies of reducing cache pilferage and reciprocal pilferage among rodents may facilitate the stability of hoarding in rodent populations (Vander Wall & Jenkins, 2003).

Hoarding behaviours usually differ between sympatric rodents, and some species may behave predominantly as scatter-hoarders or as larder-hoarders, whereas others exhibit both scatter and

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larder hoarding (Geng et al., 2017; Hollander & Vander Wall, 2004; Wang, Cao, & Zhang, 2014; Zhang et al., 2016). Larder-hoarding rodents store food items in one or a few sites (e.g. deep underground burrows) and aggressively defend them, which effectively reduces cache pilferage by competitors (Clarke & Kramer, 1994; Dally et al., 2006). In contrast, scatter-hoarding rodents distribute their caches throughout numerous small sites (containing one or a few seeds) across a large area. Therefore, aggressively defending caches appears to be difficult and even impossible for scatter-hoarding rodents. Because high rates of cache pilferage are inevitable, compensation for cache losses is vital to the survival and reproduction of scatter-hoarding rodents. Increasing seed storage or pilfering cached seeds of other rodents will be effective ways to compensate for the losses experienced by scatter-hoarding rodents (Huang, Wang, Zhang, Wu, & Zhang, 2011; Vander Wall & Jenkins, 2003). Increasing seed storage, however, is not always guaranteed, because of the limitations in seed availability due to seasonal fluctuations or mast seeding of seed production (Jansen, Bongers, & Hemerik, 2004; Kelly, 1994; Vander Wall, 2002). Thus, pilfering cached seeds of other rodents seems to be an alternative strategy for scatter-hoarding rodents to compensate for cache losses from pilferers.

The differentiation of hoarding behaviours between sympatric rodents has been well studied (Chang & Zhang, 2014; Hollander & Vander Wall, 2004; Wang et al., 2014; Zhang et al., 2016). In comparison, knowledge about the ability to pilfer caches in sympatric food-hoarding rodents is limited (Vander Wall, Enders, & Waitman, 2009; Yi, Wang, Zhang, & Zhang, 2016) and studies on pilferage behaviour among sympatric food-hoarding rodents at the community level are also rare (but see Dittel et al., 2017). Previous work has shown that the intensity of scatter hoarding (defined as number of seeds scatter-hoarded per rodent individual per unit time) and pilfering (defined as number of seeds pilfered per individual per unit time) may be highly correlated; specifically, cache-pilfering intensity is high in scatter-hoarding rodents (e.g. yellow pine chipmunks, *Tamias amoenus*) and weak in larder-hoarding rodents (e.g. golden-mantled ground squirrels, *Spermophilus lateralis*, Vander Wall et al., 2009). To our knowledge, the relationship between hoarding and pilfering intensities among sympatric food-hoarding rodents at the community level has not been quantitatively investigated. Cache pilfering depends heavily upon the rodents' olfactory ability (Hollander, Vander Wall, & Longland, 2012), and scatter-hoarding rodents could also rely on their olfactory ability to retrieve their own caches (Briggs & Vander Wall, 2004; Steele et al., 2011; Vander Wall, 2000). We thus predicted that the intensity of scatter hoarding and pilfering should be positively correlated.

In this study, we quantitatively investigated the relationship between scatter-hoarding and pilferage behaviours among four sympatric rodent species in seminatural enclosures to test our hypothesis. We predicted that rodents that showed stronger scatter-hoarding behaviour would be better pilferers than those that showed weak scatter-hoarding behaviour, and vice versa.

METHODS

Study Site and Study Species

Our study was conducted in the tropical Xishuangbanna region of Yunnan Province (21°55'N, 101°15'E), southwest China. Tropical montane evergreen broadleaf forest and tropical rainforest are the predominant vegetation types in this region (Zhu, 2006).

Four common rodent species were selected as experimental animals. Red spiny rats, *Maxomys surifer*, and Chinese white-bellied rats, *Niviventer confucianus*, are the dominant rodent species in the

tropical montane evergreen broadleaf forests and tropical rainforests (Cao, Guo, & Chen, 2017; Cao et al., 2011; Wang et al., 2014). Chestnut rats, *Niviventer fulvescens*, and yellow-bellied rats, *Rattus flavipectus*, are also common in these forests.

Previous studies have shown that seed traits significantly affect rodent foraging behaviour, including both pilfering and hoarding propensity (Hollander et al., 2012; Zhang et al., 2016). Therefore, we used two species of seeds (*Castanopsis hystrix* and *Pittosporopsis kerrii*) that differed greatly in their traits, to test whether intensity of scatter hoarding was positively correlated with cache pilfering independent of seed species. Both species are the dominant tree species in the tropical montane evergreen broadleaf forest and tropical rainforests, respectively (Lan et al., 2008; Zhu, 2006). The rodents in our study area were frequently observed to eat and hoard seeds of both species (Cao et al., 2016, 2017; Chen, Tomlinson, Cao, & Wang, 2017). The fresh seed mass of *C. hystrix* is 0.93 ± 0.04 g (mean \pm SE, $N = 53$), the dry mass is 0.64 ± 0.03 g, the seed coat is thin (0.34 ± 0.01 mm), the tannin content is low (0.15%) and the nutrient content is high (starch 78.7%, fat 0.25% and protein 3.1%; Wang et al., 2014). The fresh seed mass of *P. kerrii* is 5.57 ± 0.14 g ($N = 98$), the dry mass is 2.6 ± 0.2 g, the seed coat thickness is 0.72 ± 0.02 mm, the tannin content is low (0.27%) and the nutrient content is low (starch 38%, fat 1.8% and protein 5.6%; Cao et al., 2011).

Enclosure Experiments

Experiments were conducted in eight seminatural enclosures (10 × 10 m and 1.5 m high; see Wang et al., 2014 for details), which were located within the Xishuangbanna Tropical Botanical Garden (21°54'N, 101°15'E, elevation 550 m).

To avoid the potential influence of repeatedly removing the animals and their cached seeds from enclosures on their subsequent behaviours (Huang et al., 2011), we used different individuals in the hoarding and pilfering experiments (for sample sizes see Table 1). The top of the enclosures was covered with plastic cloth to keep rainwater out. To maintain the same environment during the experiments (Wang et al., 2014), we created wet soil conditions in the enclosures, simulating field conditions, by spraying water evenly for 5 min 1 day before the experiments commenced.

For hoarding experiments, one individual was placed in each enclosure and given laboratory food on the first day, to allow for habituation to the enclosures. On the second day, either 50 marked *C. hystrix* seeds or 40 marked *P. kerrii* were placed at the centre of the enclosure. Seeds were marked by attaching a small coded plastic tag by a thin steel thread (Xiao et al., 2006; Zhang and Wang, 2001). On the third day, we searched the whole enclosure for the seeds. Seed fates were divided into eaten in situ, eaten after being removed, scatter-hoarded (seeds dispersed away from the seed station and buried by rodents under leaf litter or in the soil in a

Table 1

The number of individuals for each rodent species used in hoarding and pilfering experiments for two seed species

Rodent species	No. of individuals	
	Hoarding	Pilfering
Using seeds of <i>Castanopsis hystrix</i>		
<i>Maxomys surifer</i>	16	8
<i>Niviventer confucianus</i>	14	8
<i>Niviventer fulvescens</i>	12	8
<i>Rattus flavipectus</i>	16	8
Using seeds of <i>Pittosporopsis kerrii</i>		
<i>Maxomys surifer</i>	18	8
<i>Niviventer confucianus</i>	16	8
<i>Niviventer fulvescens</i>	12	8
<i>Rattus flavipectus</i>	11	8

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