

## Behavioural responses of sympatric rodents to complete pilferage

Zhiyuan Huang<sup>a</sup>, Yu Wang<sup>b,1</sup>, Hongmao Zhang<sup>a,\*</sup>, Faqing Wu<sup>a</sup>, Zhibin Zhang<sup>b,1</sup>

<sup>a</sup>Laboratory of Ecology and Evolutionary Biology, College of Life Sciences, Huazhong Normal University

<sup>b</sup>State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences

### ARTICLE INFO

#### Article history:

Received 15 October 2010

Initial acceptance 6 December 2010

Final acceptance 11 January 2011

Available online 15 February 2011

MS. number: 10-00715

#### Keywords:

complete pilferage  
food hoarding  
hoarded intensity  
pilferage avoidance  
pilferage tolerance  
sex difference

Food-hoarding animals employ a variety of tactics to minimize the loss of caches to pilferers. It remains unclear, however, how these responses are affected by complete pilferage events and if differences occur between species and between the sexes within a species that adopt different hoarding strategies. We studied the behavioural responses to complete pilferage in five species that scatter-hoard or larder-hoard. Under natural conditions and within outdoor enclosures we simulated complete pilferage events by removing wild apricot, *Prunus armeniaca*, seeds hoarded by Pere David's rock squirrels, *Sciurotamias davidianus*, Korean field mice, *Apodemus peninsulae*, striped field mice, *Apodemus agrarius*, Chinese white-bellied rats, *Niviventer confucianus*, and rat-like hamsters, *Tscherskia triton*. Following pilferage, all five species increased seed removal from the source and total hoarding intensity under both natural and captive conditions, but no effect of sex was found. Pere David's rock squirrels, Korean field mice and striped field mice, which show both scatter and larder hoarding, increased scatter hoarding, but not larder hoarding. Our pilferage manipulations in the field also increased the distance that seeds were buried from the source. These findings suggest that complete pilferage may increase seed-hoarding behaviour in rodents and that scatter hoarding might be better than larder hoarding in avoiding complete pilferage in rodents that already perform both of these.

© 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Food hoarding is a strategy adopted by many species in response to temporal variation in the availability of resources (Vander Wall 1990; Tsurim & Abramsky 2004); however, hoarded food must be protected from pilfering competitors. Food pilferage is as common as food hoarding, and while this benefits the pilferer, cache loss reduces the hoarders' food storage and threatens their survival and reproductive capacity during periods of food scarcity (Wauters et al. 1995; Vander Wall & Jenkins 2003; Gerhardt 2005). Not surprisingly, food hoarders have evolved a series of strategies to deal with the risk of pilferage by competitors (reviewed by Vander Wall & Jenkins 2003; Dally et al. 2006).

According to the pilferage avoidance hypothesis, hoarders are able to adopt different tactics to minimize cache loss (Macdonald 1976; Vander Wall & Jenkins 2003; Dally et al. 2006). Birds and mammals known to hoard show a wide variety of avoidance strategies including modifying consumption and caching rates (Brotons 2000; Pravosudov & Lucas 2000; Emery et al. 2004),

recovering and moving caches repeatedly (Emery & Clayton 2001, 2004; Bugnyar & Kotrschal 2002; Emery et al. 2004), aggressively preventing access to cached items (Clarke & Kramer 1994), shifting from scatter hoarding to larder hoarding (Jenkins et al. 1995; Preston & Jacobs 2001), avoiding and delaying caching when in the presence of potential thieves (Burnell & Tomback 1985; Bugnyar & Kotrschal 2002), and spacing caches further apart or out of sight (Bugnyar & Kotrschal 2002; Dally et al. 2005; Gálvez et al. 2009). Common ravens, *Corvus corax*, rooks, *Corvus frugilegus*, and eastern grey squirrels, *Sciurus carolinensis*, also use misinformation (e.g. empty caches) to confuse potential robbers or conspecifics (Bugnyar & Kotrschal 2004; Dally et al. 2006; Steele et al. 2008).

In contrast to avoidance, the pilferage tolerance hypothesis posits that food hoarders cannot avoid or prevent pilferage and instead steal food items from other hoarders to compensate for their own losses (Vander Wall & Jenkins 2003). Under this model, pilferage is reciprocal and, as such, tolerated. Many long-term hoarding species that live in environments with high rates of cache loss may have evolved mechanisms for tolerating pilferage (Vander Wall & Jenkins 2003). For example, social animals such as jays (*Perisoreus* spp.), and solitary rodents with overlapping home ranges such as red squirrels, *Sciurus vulgaris*, field mice (*Apodemus* spp.) and agoutis (*Dasyprocta* spp.) appear to tolerate pilferage (Vander Wall & Jenkins 2003). However, this pilferage tolerance hypothesis lacks theoretical

\* Correspondence: H. Zhang, Laboratory of Ecology and Evolutionary Biology, College of Life Sciences, Huazhong Normal University, Wuhan 430079, China.

E-mail address: [hongmaozhang@gmail.com](mailto:hongmaozhang@gmail.com) (H. Zhang).

<sup>1</sup> Y. Wang and Z. Zhang are at the State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.

support and the application of game-theoretical models is not possible if animals are simply exchanging caches. For example, the best exchange that hoarders could achieve would be somewhat worse than if they simply protected their own caches. Furthermore, hoarders would do much worse if they relied only on others' caches because retrieval of these caches is generally less rewarding than protecting and retrieving their own caches.

These two models are not mutually exclusive (if they are both valid): pilferage avoidance strategies are used to minimize cache loss, and pilferage tolerance strategies are used to compensate for such loss. While this field of ecology has received much attention, little is known about how these models apply to situations involving the complete loss of an animal's food store. Only one study, on western scrub-jays, *Aphelocoma californica*, has examined how hoarders respond to unrewarded hoarding efforts and this showed that their hoarding behaviour did not cease when hoarding efforts were unrewarded and they had no choice of where to cache food (de Kort et al. 2007).

We aimed to investigate how hoarding behaviour in small rodents changes following complete cache loss. We conducted complete pilferage experiments using five sympatric rodent species residing within naturalistic enclosures and in the field. We chose Pere David's rock squirrels, *Sciurotamias davidianus*, Korean field mice, *Apodemus peninsulae*, striped field mice, *Apodemus agrarius*, Chinese white-bellied rats, *Niviventer confucianus*, and rat-like hamsters, *Tscherskia triton*, as our focal models. Pere David's rock squirrels, Korean field mice and striped field mice are known to scatter-hoard and larder-hoard food, and Chinese white-bellied rats and rat-like hamsters are known to larder-hoard only (Lu & Zhang 2008). The pilferage avoidance hypothesis predicts that when faced with complete cache loss, rodents should store seeds further away, and shift from larder hoarding to scatter hoarding to avoid cache loss. Under the same scenario, the pilferage tolerance hypothesis posits that rodents should disperse cached items at a greater rate to compensate for losses.

## METHODS

### Study Site and Subjects

Our study was conducted at the Liyuanling research station (40°00'N, 115°30'E; 1140 m above sea level) in the Donglingshan Mountains approximately 120 km northwest of Beijing city. This area has a temperate continental monsoon climate, a mean annual temperature of 10 °C and receives 600 mm of precipitation annually. The region is dominated by shrub land, secondary forest and abandoned farmland and has historically been disturbed by people and livestock. Dominant tree species include Liaodong oak, *Quercus liaotungensis*, wild walnut, *Juglans mandshurica*, wild apricot, *Prunus armeniaca*, wild peach, *Amygdalus davidiana*, and Chinese pine, *Pinus tabulaeformis*. Cultivated walnut, *Juglans regia*, is also heavily distributed throughout abandoned agricultural land. The five rodent species studied here are common throughout the study area (Li et al. 2004). This location has been the subject of much of

our previous work and further information can be obtained from Zhang et al. (2008, 2009).

We caught animals for use in the enclosure experiments from the study area, but not from areas where experiments were performed in the field (>500 m away from the field experimental plot). The number of each species and their hoarding characteristics are outlined in Table 1. We conducted trapping from June to September 2009 using steel-wire live traps (12 × 12 cm and 25 cm high). Fresh peanuts were used as bait, small pieces of cabbage were provided as a water supply and local dry leaves were provided as nest material. An iron sheet was attached on the upper side of the trap as shelter to protect from predation and sunshine (following Zhang & Zhang 2008; Zhang et al. 2008, 2009). We laid traps (20–30) every 5 m along five or six transect lines between 1800 and 1900 hours. Traps were then checked at sunrise (0600–0700 hours) and sunset (1800–1900 hours) over 3 days. Pregnant and lactating females were released immediately on site. Captured animals were carefully transferred to the laboratory using the live trap and housed individually in plastic boxes (37 × 26 cm and 17 cm high) in a room at 18–25 °C and a light-dark cycle of 14:10 h (lights on at 0530 hours). Commercial mouse chow (Keao Feed Ltd., Beijing, China), water and nest structures were provided ad libitum. Animals were acclimatized in the laboratory at least a week prior to testing. We recorded sex, mass, breeding status and age of each trapped animal. After our study, animals were retained in the laboratory and used for other studies. Animals maintained their health and weight during captivity. All field and laboratory protocols were approved by the Wuhan Municipal Science and Technology Commission and the Institute of Zoology, Chinese Academy of Sciences.

### Enclosure Experiments

These experiments were conducted from September to October (autumn) 2009 during which rodents were actively seed hoarding in preparation for winter. Twelve enclosures (4 × 3 m) were constructed in open fields around our research station using sheet iron with a thickness of 1 mm (following Lu & Zhang 2005). Each wall was placed at a depth of 30 cm underground and the height of each wall was 1 m above ground level. Each enclosure was covered with a 1 × 1 cm wire mesh that prevented focal animals escaping or other animals entering. Vegetation inside the enclosures was removed and the ground covered with 5–10 cm of sandy soil as the seed-hoarding substrate. A woody nest (20 × 30 cm and 20 cm high) and a water plate were placed in one corner of each enclosure. Seed stations (50 × 50 cm) were located at the centre of each enclosure.

Wild apricot is a common tree in secondary forest and shrub land throughout the study area (Lu & Zhang 2005). Wild apricot seeds (mean ± SD) weigh 1.2 ± 0.2 g, are 22.1 ± 1.6 mm long and 9.8 ± 0.8 mm wide (including endocarp, *N* = 50, data not shown). They ripen in the middle of July and because of their high nutritional content (53.1% crude fat, 25.5 J/g calorific value) are favoured food items that are both eaten and hoarded by the five rodent species used here (Zhang & Zhang 2008).

**Table 1**  
Species and subjects involved in a complete pilferage experiment conducted within outdoor enclosures

Species	Samples	Body length (mm)	Body weight (g)	Seed-hoarding pattern	Habit
<i>Sciurotamias davidianus</i>	8♂8♀	210.2±7.3	222.1±23.7	Scatter & Larder	Diurnal
<i>Apodemus peninsulae</i>	6♂6♀	92.0±6.2	23.5±4.1	Scatter & Larder	Nocturnal
<i>Apodemus agrarius</i>	5♂7♀	102.7±10.0	29.2±7.2	Scatter & Larder	Nocturnal
<i>Niviventer confucianus</i>	7♂5♀	128.1±11.3	62.7±10.1	Larder	Nocturnal
<i>Tscherskia triton</i>	6♂6♀	132±11.4	120.3±8.6	Larder	Nocturnal

Values are mean ± SD.

Intact wild apricot seeds used in our experiments were collected in July 2009 and marked following the tin tag method of Zhang & Wang (2001) whereby a 0.5 mm hole is drilled into the endocarp of each seed and a unique coded tin tag ( $30 \times 10$  mm, 0.1 g) is tied to each seed using a 3 cm piece of fine steel wire. This method has been used in previous studies and shown to be effective at facilitating the tracking of seed movements (Xiao et al. 2006; Gómez et al. 2008).

Animals were kept in enclosures for 72 h in total, divided into three 24 h periods of habituation, control treatment and manipulation. During habituation, 10 fresh peanuts (equal to the mean number of seeds eaten per animal per night) were supplied to each enclosure. In the second 24 h period (control), 30 tagged seeds were supplied; animals were allowed to hoard freely and the fates of the seeds were recorded. In the third 24 h period (manipulation), we removed all the seeds and their fragments (including hoarded and nonhoarded seeds) from the enclosure to simulate a complete pilferage event, after which 30 new tagged seeds were supplied for focal animals to hoard freely. After an enclosure was used, we removed all seeds and their fragments and raked the soil. A delay of 24 h was allowed between each round of experiments to minimize olfactory interference between animals.

Seed fates were recorded as 'eaten' if the kernel was consumed and the tag or seed fragments remained on the substrate or in the nest, 'scatter-hoarded' if intact and buried, 'larder-hoarded' if intact and in the nest, and 'intact after removal' if removed but remaining on the surface (Zhang & Zhang 2006, 2007). We defined 'total seed removal' as the sum of the above four categories of seeds, and 'total hoarding intensity' as the sum of scatter-hoarded and larder-hoarded seeds.

### Field Experiments

Field experiments were carried out in a 3 ha plot in a secondary broadleaved deciduous forest near the research station from September to October 2009. The area comprises a northeast-facing slope of  $45\text{--}65^\circ$  and is dominated by Liaodong oak and wild apricot trees ( $5.0 \pm 2.0$  m tall,  $N = 100$ , data not shown). Liaodong oak shrubs, wild walnut, cultivated walnut and wild peach trees are present. Canopy cover by trees and shrubs is over 80%. Three parallel transects approximately 80 m long and 20 m apart were chosen as sites for seed provision (also see Zhang & Zhang 2008; Zhang et al. 2009). Seed stations were placed every 20 m along each transect. A total of 15 seed stations were used along each trail.

We collected and marked seeds as above and a similar overall experimental design of seed provision–pilferage–seed provision was followed. Thirty tagged seeds were provided at each station between 0900 and 1000 hours. From days 1 to 5 (control), each seed station and the surrounding area (up to 50 m) were checked carefully for seeds. When a seed was located, its fate and distance from the seed station were recorded; the total number of each seed fate was recorded as the control group. We simulated complete pilferage by removing all seeds and seed fragments throughout the plot on day 6. Seeds were then provided in the same quantity and manner as during the control treatment for days 6–10; the total number of each seed fate was recorded at the end of day 10 as the

pilferage group. We repeated this experiment four times and allowed 10 days between trials. Each experimental sequence involved the provision of 900 seeds; across our four trials we provided 3600 seeds.

Seed fates were recorded as 'eaten' if the kernel was consumed and the tag or seed fragments remained on the substrate or in the nest, 'buried' if intact and buried in soil or under leaf litter, 'intact after removal' if intact seeds were removed but remained on the surface, and 'missing' if we failed to locate the seed (Zhang et al. 2008). Here we made the assumption that missing seeds were moved to burrows or cached outside the experimental area. We calculated total seed removal by summing values across all seed fates.

Following the completion of our experiments, we surveyed the area to identify the composition of rodent species present in the experimental area. We placed 40 traps along the same transects used for seed provision and repeated this for 3 days following the methods described above. Animals were released immediately after identification of species. Five rodent species were trapped in the field experimental plot (Table 2) and these species formed the focus of our enclosure experiments.

### Statistical Analysis

Total number of seeds (mean  $\pm$  SE) was used as a measure of seed-hoarding intensity and seed removal for the enclosure and field experiments. SPSS for Windows version 13 (SPSS Inc., Chicago, IL, U.S.A.) was used for statistical analyses. For data from the enclosure experiments we used a MANOVA to test the effect of pilferage and sex (and any interactions) on the number of seeds in each fate category. We used a one-way ANOVA to test the effects of our pilferage manipulation on male and female focal animals separately, to see whether there were significant effects of sex on seed fate. For data from our experiments in the field we used a Cox regression to look for differences in seed survival before and after the pilferage event. A Life Table was used to test the difference in median survival times of seeds provided at seed stations before and after pilferage. A MANOVA was used to explore differences in seed fates before and after pilferage and a one-way ANOVA was used to compare seed removal distances before and after pilferage. In the field study, very few seeds were found to be intact after removal or to have been eaten and we could not analyse these data.

## RESULTS

### Enclosure Experiments

We found an effect of simulated pilferage on the fate of seeds for Pere David's rock squirrels ( $F_{4,25} = 6.617$ ,  $P = 0.001$ ), Korean field mice ( $F_{4,17} = 6.526$ ,  $P = 0.002$ ), striped field mice ( $F_{4,17} = 4.797$ ,  $P = 0.046$ ), Chinese white-bellied rats ( $F_{4,17} = 4.458$ ,  $P = 0.045$ ) and rat-like hamsters ( $F_{4,17} = 5.783$ ,  $P = 0.029$ ), but no difference between males and females for all species (all  $P > 0.05$ ). No interaction was found between pilferage and sex for all species (all  $P > 0.05$ ).

**Table 2**  
Rodent species inhabiting the plot of our complete pilferage experiment conducted in the field

Items	<i>Niviventer confucianus</i>	<i>Apodemus peninsulae</i>	<i>Sciurotamias davidianus</i>	<i>Apodemus agrarius</i>	<i>Tscherskia triton</i>	Total
Number of animals	4	4	2	2	2	14
Percentage	28.6	28.6	14.3	14.3	14.3	100
Trap success (%)	3.3	3.3	1.7	1.7	1.7	11.7

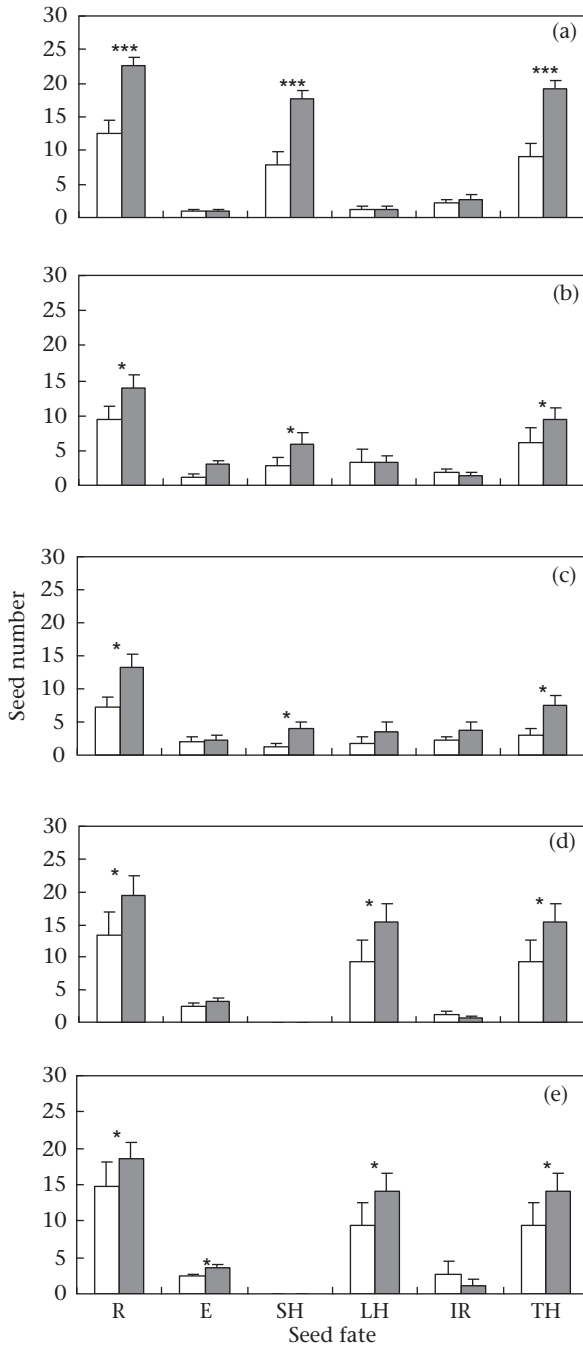
Trap days = 120.

Following pilferage, the number of total removed seeds increased for Pere David's rock squirrels ( $F_1 = 20.293$ ,  $P < 0.001$ ), Korean field mice ( $F_1 = 6.357$ ,  $P = 0.040$ ), striped field mice ( $F_1 = 4.874$ ,  $P = 0.039$ ), Chinese white-bellied rats ( $F_1 = 3.385$ ,  $P = 0.043$ ) and rat-like hamsters ( $F_1 = 6.601$ ,  $P = 0.036$ ; Fig. 1). Scatter hoarding increased following pilferage in Pere David's rock squirrels ( $F_1 = 20.446$ ,  $P < 0.001$ ), Korean field mice ( $F_1 = 5.016$ ,  $P = 0.038$ ) and striped field mice ( $F_1 = 5.318$ ,  $P = 0.032$ ); the number

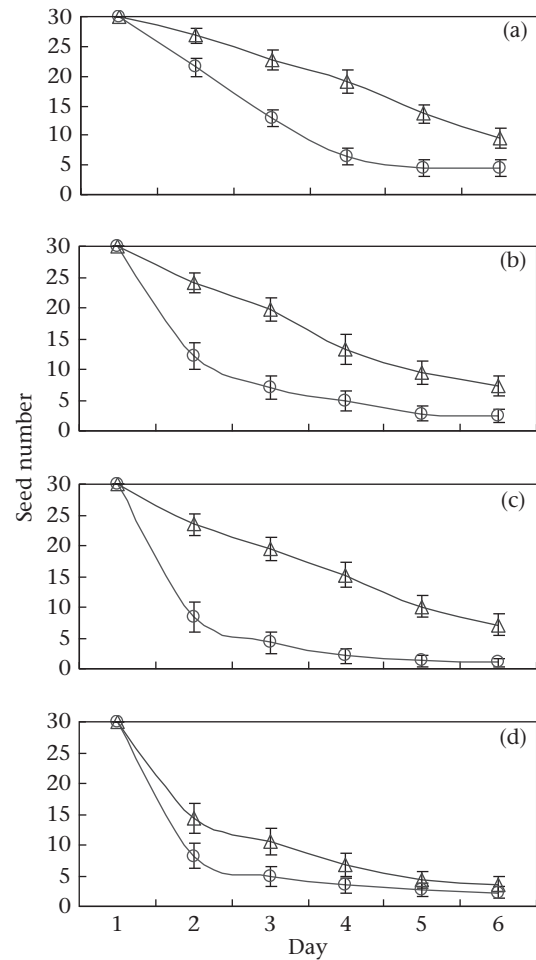
of seeds larder-hoarded (which is equal to total hoarded seeds for the two species) increased in Chinese white-bellied rats ( $F_1 = 5.398$ ,  $P = 0.030$ ) and rat-like hamsters ( $F_1 = 5.510$ ,  $P = 0.031$ ). The number of total hoarded seeds was greater following pilferage for Pere David's rock squirrels ( $F_1 = 18.556$ ,  $P < 0.001$ ), Korean field mice ( $F_1 = 6.331$ ,  $P = 0.042$ ) and striped field mice ( $F_1 = 5.599$ ,  $P = 0.028$ ). In addition, the number of seeds eaten was higher in rat-like hamsters ( $F_1 = 5.203$ ,  $P = 0.034$ ) following pilferage (Fig. 1).

### Field Experiments

An effect of pilferage on the fate of seeds and seed removal speed was found for each replicate conducted in the field (1:  $F_{3,26} = 3.614$ ,  $P = 0.026$ ; 2:  $F_{3,26} = 3.036$ ,  $P = 0.028$ ; 3:  $F_{3,26} = 9.326$ ,  $P < 0.001$ ; 4:  $F_{3,26} = 11.625$ ,  $P < 0.001$ ; Figs 2, 3). Following pilferage, the number of removed seeds increased (1:  $F_1 = 5.607$ ,  $P = 0.025$ ; 2:  $F_1 = 6.374$ ,  $P = 0.018$ ; 3:  $F_1 = 10.028$ ,  $P = 0.004$ ; 4:  $F_1 = 7.071$ ,  $P = 0.013$ ) as did the number of scatter-hoarded seeds (seeds buried in soil; 3:  $F_1 = 29.712$ ,  $P < 0.001$ ; 4:  $F_1 = 21.971$ ,  $P < 0.001$ ) and missing seeds (replicate 1 only:

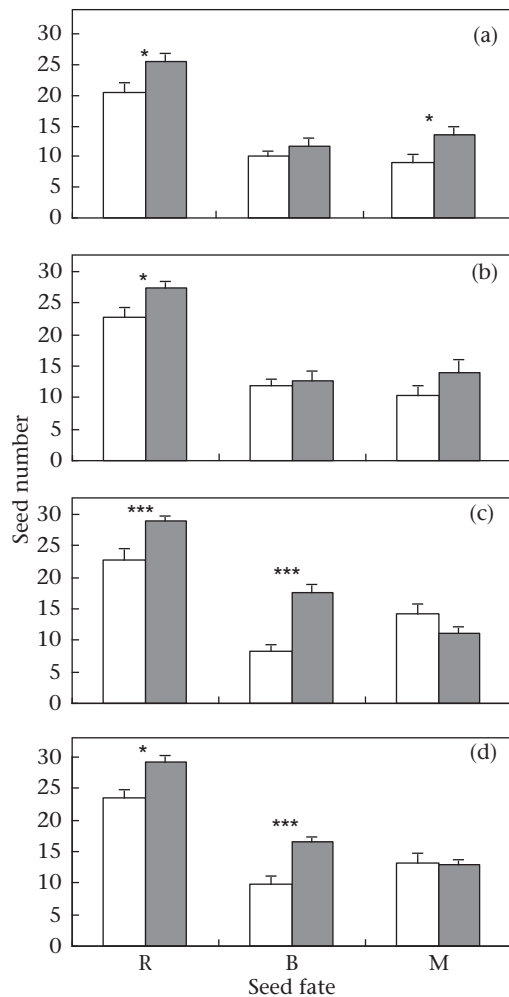


**Figure 1.** Fates of seeds handled by five rodent species before (white bars) and after (grey bars) complete pilferage in outdoor enclosures. (a) Pere David's rock squirrels, (b) Korean field mice, (c) striped field mice, (d) Chinese white-bellied rats and (e) rat-like hamsters. R: total seed removal; E: eaten; SH: scatter-hoarded; LH: larder-hoarded; IR: intact after removal; TH: total hoarding intensity. Means  $\pm$  SE are shown. \* $P < 0.05$ ; \*\*\* $P < 0.001$ .



**Figure 2.** Seed harvest by small rodents in the field before (triangles) and after (circles) their hoarded seeds were completely pilfered. (a–d) Replicates 1–4. (a) Wald = 60.923,  $df = 1$ ,  $P < 0.001$ ; median survival time in control group = 4.7 days; median survival time in pilferage group = 2.8 days. (b) Wald = 71.594,  $df = 1$ ,  $P < 0.001$ ; median survival time in control group = 3.7 days; median survival time in pilferage group = 1.8 days. (c) Wald = 140.200,  $df = 1$ ,  $P < 0.001$ ; median survival time in control group = 4.0 days; median survival time in pilferage group = 1.7 days. (d) Wald = 10.778,  $df = 1$ ,  $P = 0.001$ ; median survival time in control group = 2.0 days; median survival time in pilferage group = 1.6 days. Means  $\pm$  SE are shown.





**Figure 3.** Fates of the seeds handled by small rodents in the field before (white bars) and after (grey bars) complete pilferage. (a–d) Replicates 1–4. R: total seed removal; B: buried; M: missing. \* $P < 0.05$ ; \*\*\* $P < 0.001$ ; Means  $\pm$  SE are shown.

$F_1 = 5.873$ ,  $P = 0.022$ ; Fig. 3). Lastly, we found that scatter-hoarded seeds were buried further from the seed station following pilferage (1:  $2.3 \pm 0.6$  (150) versus  $3.2 \pm 0.8$  (176):  $F_1 = 12.838$ ,  $P = 0.001$ , control ( $N$ ) versus test ( $N$ ), mean  $\pm$  SD m; 2:  $3.5 \pm 1.7$  (177) versus  $5.6 \pm 2.4$  (191):  $F_1 = 7.750$ ,  $P = 0.010$ ; 3:  $3.5 \pm 1.4$  (125) versus  $5.7 \pm 1.9$  (264):  $F_1 = 12.124$ ,  $P = 0.002$ ; 4:  $4.1 \pm 2.3$  (148) versus  $6.6 \pm 3.4$  (249):  $F_1 = 5.312$ ,  $P = 0.029$ ).

## DISCUSSION

Our enclosure and field experiment results show that rodents hoard more seeds and harvest seeds more quickly following complete cache loss. The enhancement of food caching in response to pilferage has been reported in caching animals such as Eurasian jays, *Garrulus glandarius*, white-footed mice, *Peromyscus leucopus*, and western scrub-jays (Vander Wall & Jenkins 2003; Dally et al. 2006). In our study, all five sympatric species adopted these two strategies to compensate for complete seed loss, which suggests rodents show a general adaptive response. Dally et al. (2006), however, argued that increasing the level of caching is potentially disadvantageous for animals and impossible when pilferage is high and resources finite. For example, when surplus food is not available, hoarders are not able to increase their cache reserves above a certain level and therefore the benefits cannot offset the

extra investment with potential loss in the future. Complete food loss in our study may have been perceived by our focal rodents as increased competition and not as an increased risk of pilferage. Grey squirrels are scatter-hoarders and respond to conspecifics as competitors rather than potential pilferers, and respond to a reduction in the availability of food by increasing hoarding intensity and the distance at which they hoard food (Hopewell et al. 2008). It seems unlikely that animals would increase their hoarding intensity indefinitely if never rewarded for their hoarding efforts and one would expect animals to stop hoarding altogether. However, our results suggest that hoarding behaviour may be a compulsion and be stimulated by complete food loss. A similar result was found by de Kort et al. (2007) in western scrub-jays: their hoarding behaviours did not cease when caching efforts were never rewarded and they had no places to cache the food.

Our field experiments show that seeds were cached further away from seed stations following pilferage. This is likely to be a pilferage avoidance strategy and is similar to other studies that have found that animals at risk of having their caches pilfered space caches further apart or out of sight (Bugnyar & Kotrschal 2002; Dally et al. 2005; Gálvez et al. 2009). Seeds taken further from the source can reduce cache losses (Dally et al. 2006) and widely spaced caches have higher survival rates (Jenkins et al. 1995; Waite & Reeve 1995; Dally et al. 2006; Male & Smulders 2008). We also found that this effect increased over time and with repeated complete cache loss. However, the actual advantage of this response is not clear, as hoarders have to spend additional energy on seed transport and relocation.

We did not find a shift from scatter hoarding to larder hoarding following complete pilferage events, although three species actually increased scatter hoarding. This finding is incongruous with previous work (Dally et al. 2006). Alternating between scatter and larder hoarding reflects a trade-off between maximizing cache defence and minimizing pilferage. It is a commonly observed response in caching animals (Jenkins et al. 1995; Hurly & Lourie 1997; Preston & Jacobs 2001; Emery et al. 2004; Gerhardt 2005; Dally et al. 2006). Larder hoarding can make cache defence easier through aggressively excluding thieves (Gerhardt 2005; Dally et al. 2006) and some species such as coal tits, *Periparus ater* (Brotons 2000), eastern grey squirrels (Spritzer & Brazeau 2003) and common magpies, *Pica pica* (Clarkson et al. 1986) clump caches together perhaps to aid cache defence. Under high pilferage conditions, larder hoarding is successful only if hoarders are dominant to potential thieves (Dally et al. 2006). In contrast, scatter hoarding is regarded as a common strategy to prevent complete cache loss and is more common for subordinate animals because it is impossible for thieves to discover all scattered caches at once (MacDonald 1997; Preston & Jacobs 2001; Gálvez et al. 2009). Our failure to find an increase in larder hoarding may be because our focal animals interpreted our treatment as increased competition only: according to the rapid sequestering hypothesis (Jenkins & Peters 1992) enhanced scatter hoarding may be the result of food competition. If food supplies are limited and competition high, hoarders must sequester food more rapidly to maximize the amount they secure (Preston & Jacobs 2005).

The results from our outdoor enclosure experiments did not reveal sex differences in response to complete pilferage. Females of some rodents and birds are known to hoard more food than males, which has been interpreted as a higher female need for nutrition for reproduction (Vander Wall 1990; Burns & Horik 2007; but Steer & Burns 2008). However, very few studies have focused on sex differences in pilferage avoidance in hoarders. A somewhat related work conducted by Burns & Horik (2007) showed that female-made caches of New Zealand robins, *Petroica australis*, were recached at the same rate by both females and pilfering males, while male-made caches were recached more frequently by pilfering females.

Generally, our results show that complete food loss may increase seed-hoarding intensity in rodents and that scatter hoarding may be better than larder hoarding in avoiding complete pilferage in rodents if they already perform both scatter and larder hoarding. However, our experiments are not complete tests of the pilferage avoidance or tolerance hypothesis. According to the pilferage avoidance hypothesis, when faced with complete cache loss of scatter-hoarded seeds, rodents should decrease scatter-hoarding effort to avoid further caches loss. This prediction is not supported by our observation that rodents significantly increased scatter-hoarding intensity but not larder-hoarding intensity. Although rodents should increase scatter-hoarding intensity to compensate for cache loss, this does not necessarily support the pilferage tolerance hypothesis because these seeds were not pilfered from the caches of other rodents. It is necessary to test these two models by examining whether rodents can increase scatter-hoarding efforts by pilfering the seeds of their neighbours. In addition, some caution is required also in generalizing our results because we have not accounted for any effect of housing these animals individually in the laboratory prior to the enclosure experiments. In the field experiments we did not know exactly which species handled the seeds we provided or how each species may have influenced the behaviour of others. Given that complete food loss is likely to be relatively rare in nature, the implications of these results for natural populations deserve further consideration.

## Acknowledgments

We thank F. S. Wang, C. G. Yi and X. Y. Shang for assistance with seed collection and animal surveys. This work was partially supported by the National Natural Science Foundation of China (30800120) and State Basic Research Program of China (2007BC109102).

## References

- Brotons, L. 2000. Individual food-hoarding decisions in a nonterritorial coal tit population: the role of social context. *Animal Behaviour*, **60**, 395–402.
- Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? *Animal Behaviour*, **64**, 185–195.
- Bugnyar, T. & Kotrschal, K. 2004. Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition*, **7**, 69–76.
- Burnell, K. L. & Tomback, D. F. 1985. Stellar's jays steal gray jay caches: field and laboratory observations. *Auk*, **102**, 417–419.
- Burns, K. C. & Horik, J. V. 2007. Sexual differences in food re-caching by New Zealand robins *Petroica australis*. *Journal of Avian Biology*, **38**, 394–398.
- Clarke, M. F. & Kramer, D. L. 1994. The placement, recovery, and loss of scatter hoards by eastern chipmunks, *Tamias striatus*. *Behavioral Ecology*, **5**, 353–361.
- Clarkson, K., Eden, S. F., Sutherland, W. J. & Houston, A. I. 1986. Density dependence and magpie food hoarding. *Journal of Animal Ecology*, **55**, 111–121.
- Dally, J. M., Emery, N. J. & Clayton, N. S. 2005. Cache protection strategies by western scrub-jays *Aphelocoma californica*: implications for social cognition. *Animal Behaviour*, **70**, 1251–1263.
- Dally, J. M., Clayton, N. S. & Emery, N. J. 2006. The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, **72**, 13–23.
- Emery, N. J. & Clayton, N. S. 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, **414**, 443–446.
- Emery, N. J. & Clayton, N. S. 2004. Comparing the complex cognition of birds and primates. In: *Comparative Vertebrate Cognition: Are Primates Superior to Non-primates?* (Ed. by L. J. Rogers & G. Kaplan), pp. 3–55 The Hague: Kluwer Academic Press.
- Emery, N. J., Dally, J. M. & Clayton, N. S. 2004. Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*, **7**, 37–43.
- Gálvez, D., Kranstauber, B., Kays, R. W. & Jansen, P. A. 2009. Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory. *Animal Behaviour*, **78**, 1327–1333.
- Gerhardt, F. 2005. Food pilfering in larder-hoarding red squirrels (*Tamiasciurus hudsonicus*). *Journal of Mammalian*, **86**, 108–114.
- Gómez, J. M., Puerta-Piñero, C. & Schupp, E. W. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia*, **155**, 529–537.
- Hopewell, L. J., Leaver, L. A. & Lea, S. E. G. 2008. Effects of competition and food availability on travel time in scatter-hoarding gray squirrels (*Sciurus carolinensis*). *Behavioral Ecology*, **19**, 1143–1149.
- Hurly, T. A. & Lourie, S. A. 1997. Scatter-hoarding and larder-hoarding by red squirrels: size, dispersion, and allocation of hoards. *Journal of Mammalian*, **78**, 529–537.
- Jenkins, S. H. & Peters, R. A. 1992. Spatial patterns of food storage by Merriam's kangaroo rats. *Behavioral Ecology*, **3**, 60–65.
- Jenkins, S. H., Rothstein, A. & Green, W. C. H. 1995. Food hoarding by Merriam's kangaroo rats: a test of alternative hypotheses. *Ecology*, **76**, 2470–2481.
- de Kort, S. R., Correia, S. P. C., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007. The control of food-caching behavior by western scrub-jays (*Aphelocoma californica*). *Journal of Experimental Psychology: Animal Behavior Processes*, **33**, 361–370.
- Li, H. J., Zhang, Z. B., Wang, Y. S., Wang, F. S. & Cao, X. P. 2004. Small rodents community composition and seasonal changes of their dominant populations in the Dongling Mountain. *Acta Theriologica Sinica*, **24**, 215–222 (In Chinese with English abstract).
- Lu, J. Q. & Zhang, Z. B. 2005. Food hoarding behavior of David's rock squirrel *Sciurotamias davidianus*. *Acta Zoologica Sinica*, **51**, 376–382.
- Lu, J. Q. & Zhang, Z. B. 2008. Differentiation in seed hoarding among three sympatric rodent species in a warm temperate forest. *Integrative Zoology*, **3**, 134–142.
- Macdonald, D. W. 1976. Food caching by red foxes and some other carnivores. *Zeitschrift für Tierpsychologie*, **42**, 170–185.
- Macdonald, I. M. V. 1997. Field experiments on duration and precision of grey and red squirrel spatial memory. *Animal Behaviour*, **54**, 879–891.
- Male, L. H. & Smulders, T. V. 2008. Hyper-dispersed cache distributions reduce pilferage, a laboratory study. *Journal of Avian Biology*, **39**, 170–177.
- Pravosudov, V. V. & Lucas, J. R. 2000. The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour*, **60**, 483–493.
- Preston, S. D. & Jacobs, L. F. 2001. Conspecific pilferage but not presence affects Merriam's kangaroo rat cache strategy. *Behavioral Ecology*, **12**, 517–523.
- Preston, S. D. & Jacobs, L. F. 2005. Cache decision making: the effects of competition on cache decisions in Merriam's kangaroo rat (*Dipodomys merriami*). *Journal of Comparative Psychology*, **119**, 187–196.
- Spritzer, M. D. & Brazeau, D. 2003. Direct vs. indirect benefits of caching by gray squirrels (*Sciurus carolinensis*). *Ethology*, **109**, 559–575.
- Steele, M. A., Halkin, S. L., Smallwood, P. D., McKenna, T. J., Mitsopoulos, K. & Beam, M. 2008. Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioural deception? *Animal Behaviour*, **75**, 705–714.
- Steer, J. & Burns, K. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behavioral Ecology and Sociobiology*, **62**, 1175–1183.
- Tsurim, I. & Abramsky, Z. 2004. The effect of travel costs on food hoarding in gerbils. *Journal of Mammalogy*, **85**, 67–71.
- Vander Wall, S. B. 1990. *Food Hoarding in Animals*. Chicago: University of Chicago Press.
- Vander Wall, S. B. & Jenkins, S. H. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, **14**, 656–667.
- Waite, T. A. & Reeve, J. D. 1995. Source-use decisions by hoarding gray jays: effect of local cache density and food value. *Journal of Avian Biology*, **26**, 59–66.
- Wauters, L. A., Suhonen, J. & Dhondt, A. A. 1995. Fitness consequences of hoarding behaviour in the Eurasian red squirrel. *Proceedings of the Royal Society B*, **262**, 277–281.
- Xiao, Z. S., Jansen, P. A. & Zhang, Z. B. 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management*, **223**, 18–23.
- Zhang, Z. B. & Wang, F. S. 2001. Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). *Acta Oecologica Sinica*, **21**, 839–845.
- Zhang, H. M. & Zhang, Z. B. 2006. Effects of soil depth, cache spacing and cache size of sunflower (*Helianthus annuus*) seeds on seed discovery by Siberian chipmunk (*Tamias sibiricus senescens*). *Acta Theriologica Sinica*, **26**, 398–402 (In Chinese with English abstract).
- Zhang, H. M. & Zhang, Z. B. 2007. Key factors affecting the capacity of David's rock squirrels (*Sciurotamias davidianus*) to discover scatter-hoarded seeds in enclosures. *Biodiversity Science*, **15**, 329–336 (In Chinese with English abstract).
- Zhang, H. M. & Zhang, Z. B. 2008. Endocarp thickness affects seed removal speed by small rodents in a warm-temperate broad-leaved deciduous forest, China. *Acta Oecologica*, **34**, 285–293.
- Zhang, H. M., Chen, Y. & Zhang, Z. B. 2008. Differences of dispersal fitness of large and small acorns of Liaodong oak (*Quercus liaotungensis*) before and after seed caching by small rodents in a warm temperate forest, China. *Forest Ecology and Management*, **255**, 1243–1250.
- Zhang, H. M., Wang, Y. & Zhang, Z. B. 2009. Domestic goat grazing disturbance enhances tree seed removal and caching by small rodents in a warm-temperate deciduous forest in China. *Wildlife Research*, **36**, 610–616.