



Effects of interspecific competition on food hoarding and pilferage in two sympatric rodents

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Abstract

Food hoarding and pilferage in rodents may be regulated by intense competition between sympatric species that have similar habitats, diets and activity, but studies exploring this remain rare. Here, we used semi-natural enclosures to investigate food-hoarding and cache pilferage interactions between sympatric Korean field mice (KFM) (*Apodemus peninsulae*) and Chinese white-bellied rats (CWR) (*Niviventer confucianus*). KFM and CWR have similar diets, habitat and nocturnal activity, but the smaller KFM larder and scatter hoards and larger CWR larder hoard only. We found that KFM harvest, larder-ward and eat seeds at a greater intensity when CWR are present as an audience (present but cannot pilfer). KFM ate 11.5%, re-larder-warded 17.9% and re-scatter-warded 1.3% of their scatter-warded seeds, and ate 29.3% of their larder-warded seeds when CWR were present as pilferers. A total of 12.8% of the seeds scatter-warded and 50% of seeds directly put on the ground by KFM were pilfered by CWR. CWR did not alter hoarding intensity in the presence of KFM and their stores cannot be pilfered by KFM. These results indicate that large-sized rodent species (more dominant) significantly increase the hoarding intensity of small-sized species and show a unidirectional pilferage of seeds cached by small-sized species. The behavioural differences between these two species may reduce competition for resources and promote coexistence between sympatric rodents.

Keywords

Apodemus peninsulae, unidirectional pilferage, behavioural difference, body size, *Niviventer confucianus*, species coexistence.

1. Introduction

Food-hoarding is an economic strategy that has evolved in some rodents in order to manage fluctuations in resources (Vander Wall, 1990). Hoarders concentrate food items in one location (larder-hoarding) and/or in multiple, small piles (scatter-hoarding) (Vander Wall, 1990). Food-hoarding decisions are influenced by many factors, including competition and cache pilferage from intraspecific and interspecific individuals (Vander Wall & Jenkins, 2003; Hopewell et al., 2008). For food hoarders, competition for caches can be as important as competition for food at the food source (Vander Wall et al., 2009). Therefore, hoarders are often sensitive to competitors when caching food (Thayer & Vander Wall, 2005), and have evolved a series of strategies to reduce or prevent cache pilferage posed by intraspecific individuals (e.g., increase hoarding, cache in low density, multiple caching, shift from scatter-to larder-hoarding or vice versa, aggressive protection and cache where pilferage risk is low) (reviewed by Vander Wall & Jenkins, 2003; Dally et al., 2006; Donald & Boutin, 2011; Steele et al., 2014). While comprehensive, not too much attention has been paid to pilferage between interspecific hoarders (Leaver & Daly, 2001; Thayer & Vander Wall, 2005; Vander Wall et al., 2009; Penner & Devenport, 2011; Zhang et al., 2013).

Recently, interactions in hoarding behaviour and cache pilferage between sympatric rodents has received attention and has been associated with coexistence of sympatric rodents (Leaver & Daly, 2001; Price & Mittler, 2003, 2006; Vander Wall et al., 2009; Penner & Devenport, 2011). Heterospecific cache pilfering may be high enough to promote coexistence of similar caching species as long as mutual theft offsets individual pilfering loss (Vander Wall & Jenkins, 2003). For example, seed-cache exchanges may promote coexistence of sympatric desert rodents (Price & Mittler, 2003). However, most of these conclusions have been drawn from conditions where subjects search for observer-established caches (simulating the features of competitors' cache, Vander Wall et al., 2009), search for competitors' caches alternately (Penner & Devenport, 2011), or have been inferred from theoretical models (Price & Mittler, 2003, 2006; Vander Wall & Jenkins, 2003). Very few studies have investigated hoarder responses in the direct presence of an interspecific competitor (but see Zhang et al., 2013). Predictably, interspecific differences in pilfering success should be closely related to species-specific tactics of hoarding, cache protection, and/or cache pilfering (Penner & Devenport, 2011). However, unequivocal evidence of behavioural

differences in food-hoarding and pilferage between sympatric rodent species remains poorly understood (Price et al., 2000; Price & Mittler, 2006; Vander Wall et al., 2009).

Compared with heteroyid rodents in desert environments and subtropical forests (Reichman, 1975; Price, 1983; Swartz et al., 2010; Chang & Zhang, 2011; Zhang et al., 2013), very little attention has been directed at food hoarding and pilferage among hetero-family rodents in warm-temperate forests, possibly because these species are more ecologically diverse (Vander Wall et al., 2009). When two or more species of rodent harvest and store the same types of seeds on the ground in a similar way, and caches can be pilfered by ecologically different species, questions of how interspecific species affect each other in hoarding and pilfering become relevant. The strategies adopted by different hoarders to tolerate or avoid pilferage from other species may be crucial to their coexistence (Vander Wall & Jenkins, 2003).

At our study site in Dongliangshan, northwest of Beijing, P.R. China, Korean field mice (KFM) (*Apodemus peninsulae*) and Chinese white-bellied rats (CWR) (*Niviventer confucianus*) are common species with similar habitat (e.g., secondary forest and shrubland), diet (e.g., seeds of wild apricot, *Prunus armeniaca* and Liaodong oak, *Quercus liaotungensis*) and nocturnal activity, but have different body sizes (KFM 80–135 mm body length, 20–35 g body mass; CWR 125–195 mm body length, 45–150 g body mass) and hoarding behaviour (CWR are larder hoarders, KFM are both larder and scatter hoarders) (Li et al., 2004; Lu & Zhang, 2008; Zhang et al., 2011). KFM and CWR compete for *P. armeniaca* seeds during seedfall in July. KFM gather *P. armeniaca* seeds from the ground, scatter hoard many seeds in soil, litter or grass and larder hoard some seeds in their burrow or small caves. CWR gather *P. armeniaca* seeds from the ground and larder hoard in their burrow (Zhang, 2007), although they are known to scatter hoard some seeds in other parts of China (Chang & Zhang, 2011, 2014; Zhang et al., 2013). Therefore, these two species are ideal for studying interactions with respect to food hoarding and pilferage. Pilferage between these species appears to be unidirectional whereby CWR can pilfer scattered caches from KFM, but KFM cannot steal larder stored from CWR because CWR can physically defend them. If this prediction is true, it remains unknown how KFM avoid pilferage by CWR.

We conducted three experiments to investigate differences in hoarding behaviour and food pilferage between KFM and CWR under semi-natural

enclosure conditions. Experiment I looked at the effects of an interspecific audience (present but unable to pilfer) on hoarding behaviour in KFM and CWR. Experiment II investigated food pilferage between KFM and CWR to confirm that CWR pilfer from KFM, but KFM does not pilfer from CWR. Experiment III explored cache depth and cache density (reflected by the interval between caches) preferred by KFM in order to prevent pilferage by CWR.

These experiments were designed to test four hypotheses: (1) both species will increase hoarding intensity to increase sources in the presence of interspecific competitors (food competition hypothesis); (2) the smaller species, KFM, transfers scatter hoarded seeds into the burrow for larder-hoarding to facilitate protection (the larder defence hypothesis, Zhang et al., 2011) in the presence of CWR pilferers because the small size of their burrow entrances prevents CWR from gaining access (Zhang et al., 2011); (3) the larger species, CWR, can pilfer scatter hoarded seeds from KFM, but KFM cannot pilfer larder hoarded seeds from CWR (unidirectional pilferage hypothesis, Vander Wall et al., 2009) because CWR can aggressively defend larder stores against KFM intrusions; and (4) the smaller species, KFM, scatter hoards seeds at a certain depth and density to prevent pilferage by CWR because these buried seeds cannot be detected by CWR or are not profitable for CWR to excavate.

2. Materials and methods

2.1. Study sites

Our field station (Liyuanling, Donglingshan Mountainous area, 40°00'N, 115°30'E; 1140 m above sea level, northwest of Beijing) has been described in detail in our previous work (Zhang & Zhang, 2008; Zhang et al., 2008). KFM and CWR are common throughout the area, along with Père David's rock squirrel (*Sciurotamias davidianus*), rat-like hamster (*Tscherskia triton*), striped field mouse (*A. agrarius*) and Siberian chipmunk (*Tamias sibiricus*) (Li et al., 2004).

2.2. Animal handling

Experimental animals were trapped in 8 plots (2.5 ha, 50–100 m apart) during summer 2008 and 2012. Steel-wire live traps (12 × 12 × 25 cm) were baited with peanuts (5–10 g, also as an extraneous food supply) and covered

to protect animals from rain and direct sunlight. Small pieces of cucumber were provided as a water supply, and local dry leaves were provided as nest material (Zhang et al., 2011). No animals died during the trapping season. Two or three transects (ca. 100 m long, 20–30 m apart) within each plot were selected for trap placement. Twenty traps were placed along each transect 5 m apart. Traps were set between 18:00–19:00 h, and checked at 06:00–07:00 h for three consecutive days. Each captured individual was covered in the trap and carefully transferred to the laboratory, except for 4 pregnant females and 3 young animals that were released immediately on site. Other species of rodents were transferred to the laboratory for other experiments. Each individual was sexed, weighed, labelled, and housed in a PVC box (37 × 26 × 17 cm) with ample commercial mouse chow (Keao Feed, Beijing, P.R. China), water and nest material (wood chips). Twenty *P. armeniaca* seeds were provided to each animal every 2 days to maintain its natural diet. Approximately 50 g of peanut was provided to each animal per week as an additional nutritional supplement. Individuals of each species were housed in different rooms under ambient conditions (18–25°C) and photoperiod (12–16 h of daylight). Each individual was acclimatized to the laboratory at least 7 days prior to testing. All animals maintained their health and weight during the period of captivity and experiments, and were released to the sites where they were captured in 2008, or kept in the laboratory for other experiments in 2012. Animal trapping and our research protocols were approved by the Wuhan Municipal Science and Technology Commission (SYXK 2009-0052), Ethics Committee of Institute of Zoology, Chinese Academy of Sciences, and the local government. Our experiments were conducted in accordance with current Chinese law.

2.3. Seed preparation

Prunus armeniaca seeds are ideal for use in experiments because they are highly preferred by the focal species for consumption and hoarding and are easily obtained during July–August in the study area (Lu et al., 2005; Zhang & Zhang, 2008). The use of *P. armeniaca* seeds is described in our previous work (Huang et al., 2011; Zhang et al., 2011).

Experimental seeds were collected from more than 50 *P. armeniaca* trees near the field station during natural seedfall (July 2008 and July 2012). All seeds were then mixed to create a single composite sample and kept in a well-ventilated room to prevent mildew and fungal damage. Experimental

seeds were tin-tagged: a unique coded tin-tag (30×10 mm, 0.1 g) was tied at the basal end of the endocarp of each seed using a 3-cm piece of fine steel wire (Zhang & Wang, 2001). This method has been shown to be effective at monitoring the fate of rodent-dispersed seeds in enclosures and the field (Xiao et al., 2006).

2.4. Enclosures

We conducted these experiments in 4 semi-natural enclosures (9×9 m). Construction of the enclosures has been described in our previous work (Zhang & Zhang, 2006; Lu & Zhang, 2008). Vegetation in and around the enclosures is dominated by *Artemisia* spp., *Elymus excelsus* and *Poa* spp., 30–80 cm tall and with <60% cover. Each enclosure is covered with wire mesh (2.5×2.5 cm grid) to prevent animals from entering or leaving the enclosure.

2.5. Experimental procedures

2.5.1. Experiment I: effects of interspecific audience on hoarding behaviour in KFM and CWR

This experiment was conducted in 16 KFM (8 ♀, 8 ♂, 24.1 ± 3.7 g body mass, mean \pm SD) and 15 CWR (8 ♀, 7 ♂, 73.5 ± 12.0 g body mass) during July–August 2008. One wooden nest box ($20 \times 40 \times 20$ cm) and a water plate were placed in one corner of an enclosure. The audience animal (either a CWR or KFM), held in a steel-wire cage ($30 \times 30 \times 60$ cm) with sufficient food, water and nest material, was placed in the opposite corner to the nest box and covered with wood to shelter the animal from rain and direct sunlight. The focal animal could see, smell and partially touch the audience animal. Seed stations (50×50 cm) were located at the centre of each enclosure.

Each focal animal received the control (without audience: 24 h habituation + 24 h test) and treatment (with audience: 24 h habituation + 24 h test); roughly half the focal animals received the treatment first (KFM 4 ♀, 4 ♂; CWR 4 ♀, 3 ♂) and half the animals received the control first (KFM 4 ♀, 4 ♂; CWR 4 ♀, 4 ♂) to control for order effects. During each test an animal was introduced into an enclosure between 15:00–16:00 h, and kept in the enclosure for 2×24 h. The first 24 h were considered habituation and water and 10 untagged seeds were provided. The second 24 h were assigned for testing where 30 tagged seeds were provided (control) or 30 tagged seeds

and an audience were provided (treatment) between 15:00–16:00 h. Animals were removed and seed fates were recorded at the end of each test (between 12:00–14:00 h). At the completion of a test, enclosures were refreshed by removing all seeds and their fragments, replacing the nest box and water plate, and a break of 24 h was allowed to limit possible interactions.

Following Zhang et al. (2011), seed fates were recorded as intact *in situ* (IIS) if intact and remained at the seed station; scatter-hoarded (SH) if intact and buried; larder-hoarded (LH) if intact and in the nest; eaten (E) if the kernel was consumed and the tag or endocarp fragments remained on the substrate or in the nest; and intact after removal (IAR) if intact and put on the ground.

2.5.2. Experiment II: pilferage between KFM and CWR

This experiment was conducted using 13 KFM (6 ♀, 7 ♂, 27.8 ± 4.6 g body mass) and 12 CWR (7 ♀, 5 ♂, 73.0 ± 9.0 g body mass) from July to August 2012. When KFM were focal animals, CWR were pilferers, and vice versa. We buried two 4-l plastic buckets in opposite corners of an enclosure to serve as nests. The buckets were connected to the ground surface with a segment of PVC pipe approximately 50 cm long and either 23 mm in diameter for KFM (KFM's nest hereafter) or 40 mm in diameter for CWR (CWR's nest hereafter) following Vander Wall et al. (2009). The sizes of the PVC pipes are as large as burrow entrances for these two species in the wild and means that CWR cannot enter KFM's nest, but KFM can enter CWR's nest when empty. All experimental individuals readily accepted these nests.

Each trial included 24 h habituation + 24 h hoarding + 24 h pilferage; a 24 h break between trials was used to limit possible interactions. A focal animal was introduced into an enclosure at the beginning of the habituation period (15:00–16:00 h), when 10 untagged seeds and water were provided and the pilferer's nest was closed. After 24 h of habituation, 30 tagged seeds were placed at the centre of an enclosure as food items for hoarding by the focal animal. After 24 h of free hoarding, SH, LH and IAR seeds were recorded and mapped. Cache depth (the distance between the upper side of a buried seed and the surface) and cache interval (nearest distance between neighbouring caches, a proxy of cache density) (Male & Smulders, 2007) of all SH seeds were measured to ascertain preferred mean depth and interval of focal hoarders. After this, IIS seeds were removed, the pilferer's nest was opened and a pilferer was introduced to the enclosure. Both animals were removed 24 h later and the fates of the seeds re-handled by both animals

were recorded. When KFM were focal animals, each re-handled seed was recorded as either eaten if eaten by KFM; re-scatter-hoarded if removed out KFM's nest (LH seeds) or removed from the original location (SH and IAR seeds) and buried in soil; re-larder-hoarded if removed into KFM's nest and intact (SH and IAR seeds); or pilfered by CWR if eaten by CWR or removed into CWR's nest (SH and IAR seeds). KFM's LH seeds could not be pilfered by CWR because of the small entrance size of KFM's nests. When CWR were focal animals (larder hoarders), each re-handled seed was recorded as either eaten if eaten by CWR; re-larder-hoarded if removed into CWR's nest and intact (IAR seeds only); or pilfered by KFM if removed from CWR's nest (LH seeds) or removed from the original location (IAR seeds) and then buried in soil, eaten, or moved into KFM nests. Species-specific scrapes and dental marks on endocarps allowed us easily to determine which species consumed a seed because the openings on the endocarp left by CWR are longer in length, shorter in width, and have larger dental marks than those left by KFM (Lu & Zhang, 2004; Zhang & Wang, 2009). We assumed that all scatter-hoarded caches were made by KFM because CWR are strictly larder hoarders in our study area (Lu & Zhang, 2008; Huang et al., 2011; Zhang et al., 2011), although they scatter-hoard some seeds in other parts of China (Chang & Zhang, 2011; Zhang et al., 2013). No animals removed seeds from their own nests in this and previous studies (Huang et al., 2011; Zhang et al., 2011). We were unable to determine which species was responsible when a SH or IAR seed was re-IAR, but this was ignored because only two IAR seeds underwent this fate across our experiment.

2.5.3. Experiment III: the cache depth and interval preferred by KFM to CWR pilferage

This experiment was conducted using 12 CWR (6 ♀, 6 ♂, 71.6 ± 8.7 g body mass) in September 2012. From experiment II we knew that CWR could pilfer a few KFM scatter-hoarded seeds only, allowing us to hypothesize that CWR can rarely find a cache when its depth is greater than the KFM-preferred cache depth, or when the cache interval is greater than the KFM-preferred cache interval. We established five levels of cache depth (0.0 cm, put on ground surface directly; 1.0 cm; 2.5 cm, KFM preferred; 5.0 cm; and 8.0 cm) and five levels of cache interval (5.0 cm; 20.0 cm; 50.0 cm, KFM preferred; 100.0 cm; and 150.0 cm). We assumed that these caches would pose different levels of difficulty to CWR. Each trial comprised one night (ca. 14 h) of free cache foraging whereby an animal was

introduced into an enclosure in the evening (18:00–18:30 h) and removed the next morning (08:00–08:30 h). Before each trial, 25 caches (one seed per cache) at one level of depth (constant interval of 50.0 cm, KFM preferred) or interval (constant depth of 2.5 cm, KFM preferred) were established around the centre of an enclosure, and their locations were mapped. Five peanuts were placed on the surface at the centre of an enclosure to determine where subjects were visiting. A nest box and a water plate were put in one corner of the enclosure. All caches discovered by CWR were recorded at the end of a trial, and a 24 h break was allowed to limit interactions between trials. A cache was discovered by CWR if it was dug out. Each individual experienced all levels of cache depth and interval following a random order.

2.6. Statistical analyses

Seed numbers were analysed with SPSS v16.0 (SPSS, Chicago, IL, USA). Count data were first tested for normality using the Shapiro–Wilk test and, if significantly different from normality, $\log(x + 1)$ transformed to achieve normality (also see Chang & Zhang, 2011). We combined data from males and females in each analysis to increase sample size because no significant differences were found between sexes (two independent samples *t*-tests). One-way ANOVA was used to determine differences in KFM and CWR behaviour (each seed fate) when an observer was or was not present. One-way ANOVA, including LSD for pairwise comparisons, was also used to test differences in cache recovery by CWR across different levels of cache depth and interval. All statistical tests were two-tailed, and differences were significant when $p < 0.05$.

3. Results

KFM increased seed harvest ($F_{1,30} = 5.238$, $p = 0.029$, one-way ANOVA), larder-hoarding ($F_{1,30} = 6.853$, $p = 0.014$) and eating ($F_{1,30} = 4.676$, $p = 0.053$) in the presence of a CWR audience (Figure 1a), whereas CWR did not alter hoarding behaviour in the presence of a KFM audience (all $p > 0.05$) (Figure 1b).

KFM ate 11.5% (9/78, 0.7 ± 0.9 , mean \pm SD, $N = 13$), re-larder-hoarded 17.9% (14/78, 1.2 ± 1.6), and re-scatter-hoarded 1.3% (1/78, 0.1 ± 0.3) of their primary scatter-hoarded seeds, whereas they ate 29.3% (29/99, $2.2 \pm$

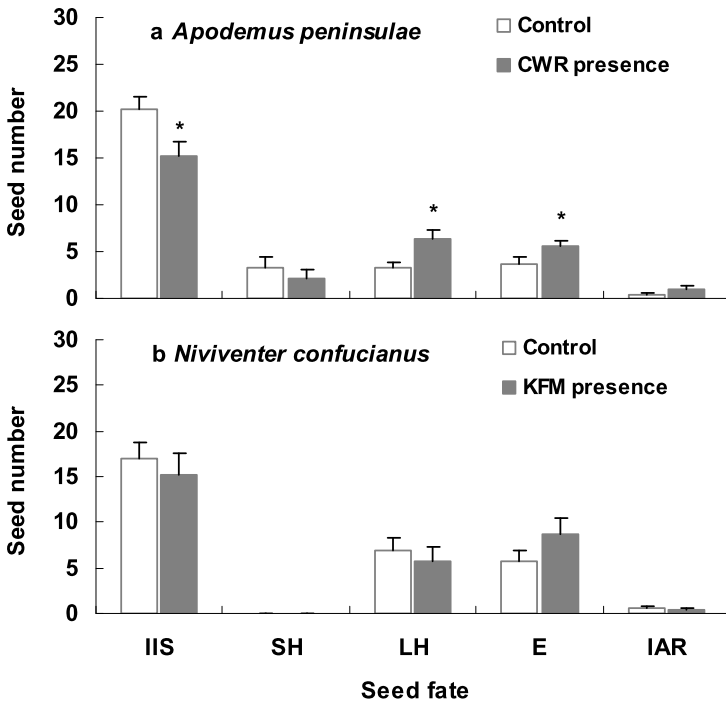


Figure 1. Effects of interspecific presence on seed-hoarding behaviour in Korean field mice (KFM) (*Apodemus peninsulae*) (a) and Chinese white-bellied rats (CWR) (*Niviventer confucianus*) (b) under enclosure conditions. Seed fates: IIS, intact *in situ*; SH, Scatter-hoarded; LH, Larder-hoarded; E, eaten; IAR, intact after removal. Data are mean \pm SE (* $p < 0.05$).

2.1) of their primary larder-hoarded seeds with CWR present as pilferers (Table 1). A total of 12.8% (10/78, 0.8 ± 1.2) of scatter-hoarded seeds and 50.0% (6/12, 0.5 ± 1.0) of intact after removal seeds by KFM were pilfered by CWR (Table 1). CWR ate 39.8% (37/93, 3.7 ± 3.5 , $N = 10$) of their primary larder-hoarded seeds when KFM were introduced as pilferers. CWR's larder-hoarded seeds were not pilfered by KFM (Table 2).

The number of caches discovered by CWR decreased with increasing cache depth ($F_{4,55} = 111.709$, $p < 0.001$, One-way ANOVA) and interval ($F_{4,55} = 17.422$, $p < 0.001$) (Figure 2). CWR rarely discovered caches greater than 2 cm deep and 50 cm apart, which are approximately equal to the mean cache depth (2.1 ± 1.0 cm, mean \pm SD, $N = 78$) and mean cache interval (51.3 ± 72.7 cm) utilised by KFM (Figure 2).

Table 1.

Cache pilferage of wild apricot (*Prunus armeniaca*) seeds by Korean field mice (KFM) (*Apodemus peninsulae*) under enclosure conditions.

	Seed fate	Items	Total	Re-handled by KFM			Pilfered by CWR
				E	Re-SH	Re-LH	
KFM (N = 13)	SH	N (%)	78 (100.0)	9 (11.5)	1 (1.3)	14 (17.9)	10 (12.8)
		Mean ± SD	6.0 ± 6.0	0.7 ± 0.9	0.1 ± 0.3	1.2 ± 1.6	0.8 ± 1.2
		Range	0–21	0–3	0–1	0–4	0–3
	LH	N (%)	99 (100.0)	29 (29.3)	0	–	0
		Mean ± SD	7.6 ± 8.8	2.2 ± 2.1	0	–	0
		Range	0–28	0–7	0	–	0
	IAR	N (%)	12 (100.0)	0	0	0	6 (50.0)
		Mean ± SD	0.9 ± 1.0	0	0	0	0.5 ± 1.0
		Range	0–3	0	0	0	0–3

SH, scatter-hoarded; LH, larder-hoarded; IAR, intact after removal; E, eaten; Re-SH, re-scatter-hoarded; Re-LH, re-larder-hoarded; CWR, Chinese white-bellied rats (*Niviventer confucianus*); –, not applicable.

4. Discussion

When an interspecific competitor is present, KFM increase the harvest, hoarding and consumption of seeds, supporting our food competition hypothesis; however, CWR did not greatly alter hoarding behaviour, thereby rejecting the food competition hypothesis. The enhancement of harvest and

Table 2.

Cache pilferage of wild apricot (*Prunus armeniaca*) seeds by Chinese white-bellied rats (CWR) (*Niviventer confucianus*) under enclosure conditions.

	Seed fate	Items	Total	Re-handled by CWR			Pilfered by KFM
				E	Re-SH	Re-LH	
CWR (N = 10)	LH	N (%)	93 (100.0)	37 (39.8)	0	–	0
		Mean ± SD	9.3 ± 8.9	3.7 ± 3.5	0	–	0
		Range	1–30	0–11	0	–	0
	IAR	N (%)	2 (100.0)	0	0	0	0
		Mean ± SD	0.2 ± 0.6	0	0	0	0
		Range	0–2	0	0	0	0

SH, scatter-hoarded; LH, larder-hoarded; IAR, intact after removal; E, eaten; Re-SH, re-scatter-hoarded; Re-LH, re-larder-hoarded; KFM, Korean field mice (*Apodemus peninsulae*); –, not applicable.

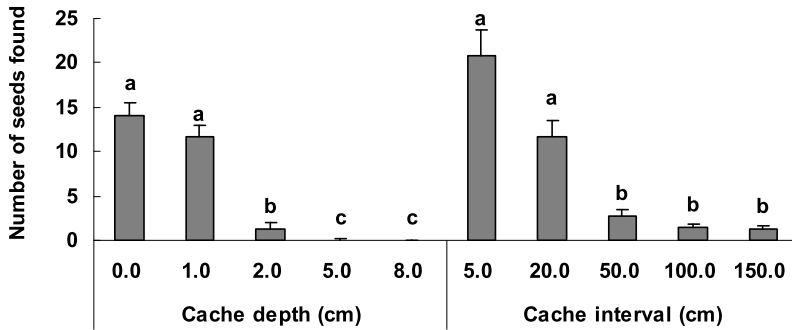


Figure 2. Caches discovered by Chinese white-bellied rats (*Niviventer confucianus*) at different levels of cache depth and interval. All data are mean \pm SE. Bars with different letters are significant differences ($p < 0.05$). A total of 25 caches were established in each category.

hoarding is an important response to pilferage by conspecific and interspecific competitors (Vander Wall & Jenkins, 2003; Dally et al., 2006). KFM increases harvest and hoarding intensity when there is a conspecific audience (Zhang et al., 2011), when their caches are completely lost (Huang et al., 2011), or when there is a CWR audience (this study). These may be strategies to offset pilferage or simple competition to rapidly sequester food sources (Zhang et al., 2011). However, it will only provide an advantage when resources are beyond a maximum level at which hoarders can harvest and cache enough food to compensate for the costs of harvest and hoarding, and loss from pilfering (Dally et al., 2006). If not, hoarders may still be more likely to protect their own caches. Increased eating was another response used by KFM in the presence of CWR. KFM also increase consumption under elevated pilferage risk (Zhang et al., 2011) or when suffering from complete cache losses (Huang et al., 2011). Hoarders may gain definite advantages from increased eating because they are able to generate internal energetic reserves when pilferage risks are high (Dally et al., 2006). However, it is unlikely that this increased energy intake allows substantially higher rates of internal energy storage in smaller-bodied species (Blem & Pagels, 1984). Increasing consumption behaviour should not replace, but be used in conjunction with external reserves (Dally et al., 2006). CWR increase harvest and hoarding intensity in the presence of a conspecific individual (Zhang et al., 2011), following complete cache loss (Huang et al., 2011) or when faced with a large (*T. triton*, unpublished data) or similar (*R. flavipectus*, Zhang et al., 2013) sized interspecific competitor, but not in the presence of a small KFM (this study). It appears that increasing hoarding in

response to competitors and pilferers is context-dependent (e.g., body size, social status and competitor species) in CWR (also see Eurasian jays, *Garulus glandarius*, and Western scrub-jays, *Aphelocoma californica*, reviewed by Dally et al., 2006).

It is predicted that hoarders who adopt both scatter- and larder-hoarding strategies and that cannot adequately defend their caches (e.g., small in body size) should increase scatter-hoarding intensity to avoid complete cache loss under high pilferage risk (Jenkins et al., 1995; Preston & Jacobs, 2001). However, our findings are inconsistent with this prediction because small KFM increased larder-hoarding in the presence of the larger CWR (also see example in Preston & Jacobs, 2001), supporting the larder defence hypothesis that larder-hoarding is more suitable for cache protection in KFM (Zhang et al., 2011). KFM also respond to conspecific individuals by increasing larder-hoarding (Zhang et al., 2011). That larder hoards of small-bodied rodents may be unavailable to larger species was also observed by Jenkins & Breck (1998). In the field, KFM often larder-ward seeds in burrows and small caves that prevent potential thieves (e.g., CWR) from gaining access to these seeds due to the small size of the entrance (H.M.Z., pers. observ.).

In the semi-natural environment created here, unidirectional pilferage was found whereby CWR pilfered seeds scatter-hoarded by KFM, but did not have its own seeds pilfered by KFM thus supporting our unidirectional pilferage hypothesis. CWR have definite aggressive advantages (Zhang et al., 2011) and can pilfer scatter-hoarded stores by KFM. We also found that CWR did not alter hoarding behaviour in the presence of KFM, but KFM increased harvest, eating and hoarding behaviour in the presence of CWR, and transition from scatter-hoarding to larder-hoarding under pilfering pressure from CWR. These results emphasize the unidirectional food pilferage relationship between CWR and KFM. Martin & Martin (2001) also argued that one species makes most of the compensatory adjustments to reduce competition, whereas the other species may make little or no behavioural changes when competition is strongly unidirectional. Unidirectional pilferage between sympatric small rodents has been detected in other studies (Leaver & Daly, 2001; Vander Wall et al., 2009; Penner & Devenport, 2011). For example, the smaller least chipmunk (*Tamias minimus*) locates caches of the larger Eastern chipmunk (*T. striatus*) more quickly and with less effort under semi-natural conditions (Penner & Devenport, 2011). Vander Wall & Jenkins (2003) argue that high cache pilferage between species can evolve from

and promote the coexistence of sympatric species, as long as mutual theft offsets individual pilfering losses. However, under unidirectional pilferage, one species has a definite pilfering advantage over the other, and the vulnerable species cannot compensate for cache loss by pilfering the food stores of competitors. Unidirectional pilferage between sympatric species may be common, but the behavioural mechanisms have seldom been characterized (Vander Wall et al., 2009).

We found that cache discovery by CWR decreased with increasing cache depth and interval, consistent with other studies (Vander Wall, 1993; Geluso, 2005; Zhang & Zhang, 2006; Sun & Zhang, 2013). Very few caches were moved by CWR when the cache depth or cache interval was greater than those KFM preferred, supporting our 4th hypothesis that burying seeds below a certain depth and density is an adaptive strategy by KFM to prevent CWR pilferage (also see yellow pine chipmunk, *T. amoenus*, Vander Wall et al., 2009). Success pilfering is dependent on the pilfering strategies of thieves and cache protection strategies of the owners, and natural selection favours strategies that both enhance cache protection and enhance cache pilfering (Dally et al., 2006; Penner & Devenport, 2011). It is generally believed that food hoarding evolves when hoarders are more likely than naive individuals to retrieve their own caches (Andersson & Krebs, 1978) or if cache pilferage is at some acceptably low level at which hoarders can tolerate cache losses (Vander Wall & Jenkins, 2003). Here, only a small number of scatter-hoarded KFM caches were pilfered by CWR because CWR appear to be unable to detect caches at a greater depth and interval than those preferred by KFM. These results suggest that KFM suffer pilferage by CWR at a low level, and are more likely than CWR to retrieve their stores. For small nocturnal rodents, odour cues are especially crucial for cache detection and are likely stronger when caches are shallow (Geluso, 2005) or at a high density (Sun & Zhang, 2013). Deeply buried seeds represent a high cost of exploration, extraction and elevated predation risk (Vander Wall, 1993). Instead of pilfering caches from KFM, CWR prefer to rapidly harvest seeds from the ground and shallow soil, especially when the seed source is ephemeral (the peak season of seedfall of wild apricot is about one week in our study area; Lu et al., 2005) and competition is high.

Sympatric species with similar habitats, diets and activity can lead to intense competition (Vander Wall et al., 2009) and raise questions about species coexistence (Price et al., 2000; Leaver & Daly, 2001). As well as

spatial or temporal heterogeneity in resource availability (Kotler & Brown, 1988) and different physiological tolerances (Jaeger, 1971), differences in foraging behaviour (e.g., food hoarding, food pilferage, microhabitat selection) have been suggested as mechanisms to facilitate coexistence between species (Price et al., 2000; Leaver & Daly, 2001; Price & Mittler, 2003, 2006; Vander Wall et al., 2009; Swartz et al., 2010; Baudoin et al., 2013; Zhang et al., 2013). For example, heteromyid rodents (Merriam's kangaroo rat, *Dipodomys merriami*, pale kangaroo mouse, *Microdipodops pallidus*, and little pocket mouse, *Perognathus longimembris*) may contribute to spatial heterogeneity of available resources by caching seeds in different microhabitats that reduces cache pilferage by other species and benefits coexistence (Swartz et al., 2010). Theoretical models also demonstrate that species coexistence is facilitated when cache exchange occurs between heteromyids (Price & Mittler, 2003) and when species exhibit differences in their ability to pilfer caches (Price & Mittler, 2006). Here, KFM larder-hoarded seeds in burrows and scattered seeds at a certain depth and interval where it is difficult for CWR to detect and pilfer. CWR larder-hoarded seeds in burrows only and these were not accessed by KFM. KFM transitioned scattered caches to burrows for larder-hoarding under pilferage risk (Zhang et al., 2011; this study) or following pilferage (Huang et al., 2011; this study). These differences in caching may reduce competition and contribute to the coexistence of these two species. Species coexistence is complicated and associated with many factors, and the exact mechanisms of coexistence between KFM and CWR require further investigation.

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