ORIGINAL ARTICLE

Visual and auditory cues facilitate cache pilferage of Siberian chipmunks (*Tamias sibiricus*) under indoor conditions

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Running Head: cache pilferage by visual/auditory cues

Abstract

In the struggle for survival, scatter-hoarding rodents are known to cache food and pilfer the caches of others. The extent to which rodents utilize auditory/visual cues from conspecifics to improve cache-pilfering is unknown. Here, Siberian chipmunks (*Tamias sibiricus*) were allowed to search for caches of *Corylus heterophylla* seeds (man-made caches and animal-made caches) after experiencing cues from a conspecific's cache-searching events. For each type of cache, three experimental scenarios were presented: 1) alone (control), 2) auditory/visual (hearing and seeing conspecific's cache-searcing events) and 3) auditory only (hearing conspecific's cache-searcing events only) with random orders. The subjects located man-made caches faster, harvested more caches, and hoarded more seeds both in the auditory/visual and the auditory only treatments compared to the control, while scatter-hoarded more seeds in the auditory/visual treatment, but larder-hoarded more seeds in the auditory only treatment. Compared to the control, the animals spent less time locating animal-made caches, harvested more caches, ate less seeds, larder-hoarded more seeds and hoarded more seeds in total both in the auditory/visual and the auditory only treatments, while ate more seeds and hoarded less seeds in total in the auditory only treatment than in the auditory/visual treatment. The results also show that females spent less time locating the animal-made caches, but they scatter-hoarded fewer seeds than males in the auditory/visual treatment. To our best knowledge, this is the first report that visual and/or auditory cues of conspecifics improve cache-pilfering and hoarding in rodents.

Key words: cache pilferage, cache protection, food hoarding, observational spatial memory, rodents

INTRODUCTION

Hoarding food for future use is an adaptive strategy to fluctuations of food resource availability in animals (e.g., birds and mammals), and is beneficial for survival and reproduction (Vander Wall 1990). Hoarding behaviour evolves in environments when hoarded food items are retrieved and eaten during periods of food scarcity, thereby improving hoarders' fitness (Vander Wall 1990). Cache loss due to pilferage by both inter- and intra-specifics is an important evolutionary factor of food-hoarding behaviour (Andersson & Krebs 1978; Dittel *et al*. 2017). In the cacher-pilferer arms race, both cachers and pilferers are sensitive to this antagonistic interaction and take precautions against opponents (Vander & Jenkins 2003; Dally *et al*. 2006; Grodzinski & Clayton 2010).

Cache protection strategies in mammals and birds have been extensively studied (reviewed by Dally *et al*. 2006; Grodzinski & Clayton 2010). Food hoarders have shown one or more strategies that are not mutually exclusive to reduce cache loss when faced with the likelihood of pilferage. Cache protection strategies adopted by food hoarders are often concerned with ways to limit or invalidate the information that a potential pilferer has gathered (e.g., visual information and spatial memory, Grodzinski & Clayton 2010). For example, 1) increasing scatter-hoarding, ceasing or delaying caching, and/or increasing cache vigilance to decrease probability of food loss (reviewed by Dally *et al*. 2006); 2) caching food far away from the source to reduce competition and spacing caches to reduce density dependent loss (Galvez *et al*. 2009; Zhang *et al*. 2014); 3) making 'false' caches to confuse potential pilferers at the time of caching (Steele *et al*. 2008); 4) storing food in unfavorable places (e.g., out of tree canopy cover, open grassland or shrub edge) to avoid high rates of pilferage (Muñoz & Bonal 2011; Zhang *et al*. 2013; Steele *et al*. 2014, 2015); 5) hiding food in secret places and repeatedly caching items to invalidate pilferers' sensory information while they are observed (Dally *et al*. 2004, 2005); and/or 6) concealing auditory information from potential pilferers (Stulp *et al.* 2009).

Cache pilfering from other individuals has been far less studied than cache protection in food-hoarding animals (reviewed by Dally *et al*. 2006). Some birds perform random search, while some mammals (e.g., small rodents) rely on olfactory ability to search for caches of others (Vander Wall 1990; Yi *et al*. 2016a; Grodzinski & Clayton 2010). David's rock squirrels (*Sciurotamias davidianus*) can discover more than 60% of buried nuts (*Juglans regia*) within 24 hours using primarily olfactory cues (Zhang & Zhang 2007). Seeds with strong odors or those buried in wet soil are more likely to be discovered by rodents (Downs & Vander Wall 2009; Hollander *et al*. 2012; Yi *et al*. 2016a). However, animals relying on random searching and olfactory cues to search for caches are less efficient than cache owners because they have no prior knowledge of cache location. Observational memory would be strongly selected by the cacher-pilferer arms race, because pilferers, similar to cache owners, observe and encode cachers' caching events, and then use this observational memory to pilfer caches in the absence of owners (Grodzinski & Clayton 2010). Several species of birds are able to locate caches of other individuals using observational memory (e.g., Mexican jays *Aphelocoma ultramarine* and Pinyon jays *Gymnorhinus cyanocephalus* Bednekoff & Balda 1996 a, b; western scrub-jays *A. califonica*, Watanabe & Clayton 2007; ravens *Corvus corax*, Scheid & Bugnyar 2008; but not in black-capped chickadees *Poecile atricapillus*, Baker *et al*., 1988). For example, western scrub-jays spent much more time observing individuals who are caching than those not caching, and searching locations where there is high potential for caching rather than places not suitable for caching, and they subsequently locate caches accurately (Grodzinski *et al*. 2012). Monkeys, apes and humans are well known users of observational memory to pilfer food from others (Byrne & Whiten 1988; Melis *et al*. 2006). Evidence suggests that rats (*Rattus norvegicus*) have episodic memory, remembering when, what, and where foods were encountered (Babb & Crystal 2005, 2006; Roberts 2006). Yi *et al*. (2016b) reported that Siberian chipmunks (*Tamias sibiricus*) can use memory to conserve their own caches by selectively pilfering caches of others. The use of

observational memory in cache-pilfering is highly efficient because pilferers, like the cache owners, know the

cache location information; however empirical evidences are rare in wild rodents.

Potential pilferers may also use auditory cues created by cachers to pilfer caches. Use of available

auditory information for predator avoidance, foraging and social communication has been well documented in

mammals and birds (reviewed by Davies *et al*. 2012). For example, cotton rats (*Sigmodon hispidus*) and

eastern chipmunks (*T. striatus*) increase perceive predation risks and compromise their patch assessment

performance when they eavesdrop on the alarm vocalization of a sympatric species (e.g., blue jays, *Cyanocitta*

cristata, eastern tufted titmouse, *Baeolophus bicolor*) (Schmidt *et al*. 2008; Felts & Schmidt 2010). Several

studies have shown that auditory cues are directly involved in the evolutionary interaction of the

cacher-pilferer arms race (e.g., Schmidt & Ostfeld 2008; Stulp *et al*. 2009). When western scrub-jays are

heard but not seen by a conspecific individual, they might conceal auditory information of the caching events

by caching proportionally less food items in noisy substrate (small pebbles) compared to food items in

soundless substrate (soil) (Stulp *et al*. 2009). Gray squirrels (*Sciurus carolinensis*) reduce cache value and

only forage at the sites with high pilferage risks in the presences of blue jays' calls, suggesting that this

species can assess site-specific risks of cache pilfering and alter their caching behaviour to reduce the

likelihood of pilferage through eavesdropping (Schmidt & Ostfeld 2008). However, very few studies have

actually documented whether animals pilfer caches from others using auditory cues provided by cache

owners.

Here, we used Siberian chipmunks (*Tamias sibiricus*) as a study model of food-hoarding behaviour to test

if this species can improve the probability of cache-searching and pilfering using visual and/or auditory cues

created by conspecifics. If visual and auditory cues of conspecifics can help Siberian chipmunks improve food

harvest, the tested animals (hereafter "observers") will spend less time to locate caches and hoard more food

in a given time when they have previous experiences of hearing and/or seeing food-hoarding events of conspecifics (hereafter "performers"). To test this hypothesis, observers were allowed to search for man-made caches and performer-made caches separately under three different conditions: 1) control (not seeing or hearing performer's cache events); 2) auditory/visual treatment (after seeing and hearing a performer's cache events); and 3) auditory only treatment (after hearing a performer's cache events). We expected to determine the minimum information required by the observers (pilferers) to successfully pilfer caches of performers, and whether this is context dependent.

MATERIALS AND METHODS

Study animals

The Siberian chipmunk is a common diurnal species in northern China, with a size range of 110 – 125mm in body length and 75 – 120g in body weight. In the field, Siberian chipmunks store seeds directly in burrow and/or firstly scatter hoard seeds in the soil and litter around the seed sources and subsequently transfer a large portion of these seeds into their burrows, mediating dispersal and regeneration of large-seeded plant species (*Quercus* spp., *Pinus* spp., *Corylus* spp.) (Yang *et al*. 2012; Yi *et al*. 2012, 2016a, b). Siberian chipmunks' caches usually suffer from pilfering by inter- and intra-specific individuals, whereas they pilfer caches from other individuals also (Yi *et al*., 2012, 2016a). Yi *et al*. (2016a, b) reported that Siberian chipmunks can use spatial memory and olfaction cues locating and managing their own caches, but it is unclear if they can use conspecific's information from caching activities in order to pilfer from others. Experimental animals were bought from the Wuhan Dijiao Pet World (Dijiao Road, Jiangan District, Wuhan) in August 2015 (16♂, 14♀, 107.2 ± 4.6 g body weight, mean ± SD) and in July 2016 (15♂, 15♀, 104.3 ± 6.8 g body weight) separately. These animals were captured in the field in northern China, with no additional information about how and

where they were trapped, or any of their prior experiences. Body weight of the animals used in the experiments did not change more than ten grams during the tests. The animals were individually housed in steel frame cages (L× W ×H = 40 cm × 30 cm × 30 cm) with a nest box (L× W ×H = 15 cm × 10 cm ×10 cm) in one corner. Animals were allowed to acclimate for at least one week before experiments and maintained on a photoperiod of 12:12 h light: dark and a temperature of 20 – 25 ℃. Tap water, peanuts, Asian hazel (*Corylus heterophylla*) seeds and bedding materials (wood filings) were provided *ad libitum*. Experiments were conducted during August to October when it is favorable for Siberian chipmunks to hoard seeds in the field. After testing, the animals were kept in captivity for other studies. The animal handling procedures were approved by the Science and Technology Department of Hubei Province, China (SYXK(é) 2015-0052), and the Central China Normal University.

Experimental arena

All tests were carried out in two indoor arenas (two rooms separated by a monitor room) (Fig. 1). Each room (L× W ×H = 4.0 m × 3.0 m × 3.5 m) had white walls and ceiling with natural light from windows. Two fluorescent lights (50-W each) were hung on the ceiling to supplement light from 0600 to 1800 hours each day. A video camera was suspended in one corner of the room (2.5m high from the ground) with a monitor in an adjacent room (between the two arenas), allowing experimenters to monitor the animals without interference. The ground was covered with a 10 cm deep layer of sandy soil to allow seed-caching. A water plate and a wood nest box (L× W ×H = 30 cm × 20 cm × 20 cm) containing cotton and nesting materials were placed in one corner of the arena. Eight additional wood boxes (L× W ×H = 30 cm × 30 cm × 15 cm) were evenly placed in the arena as shelter places for animals. Three bricks were placed 30 cm apart at the centre of the arena to serve as visual cues for cache sites. Ten seeds of *C. heterophylla* were buried 10 cm apart and 2 cm depth in the soil around each brick as food source for experimental animals (hereafter "man-made caches")

(Fig. 1). Every site in the arena could be located using a plane coordinate system on the monitory screen, allowing us to locate caches. At the end of each test, the arenas were cleared by moving away all of the seeds and seed-fragments, replacing the water plate and nest, and clearing feces. To reduce interference from olfactory cues between trials, 200 ml of alcohol was evenly sprayed on the ground surface and allowed to ventilate 24 hours.

Experimental procedures

Man-made caches searching

The man-made caches searching experiments were conducted in 2015. Here, the tested animals were allowed to locate man-made caches under the conditions of without (control), hearing and seeing (auditory/visual treatment), and hearing only (auditory only treatment) a conspecific's cache-searching performance in a given time. We know that auditory / visual cues can help the experimental animals locating the man-made caches by comparing cache-searching time and cache harvest proportion between treatments and control.

All of the animals were pre-screened as candidates for the experiments in the arenas by allowing them to search for the buried seeds within a 24-hour period. Four individuals ($2\male$, $2\female$, 106.4 ± 4.4 g body weight) that rapidly located the man-made caches and established new caches were selected as performers in the tests and given three days of extra training. Repeated training ensured performers to easily locate the man-made caches and establish enough new caches during each test, and therefore providing the cues of cache-location to observers. Each performer was repeatedly used with at least three days of break between two trials. Twenty-four animals that consistently located caches and performed hoarding behaviour were selected as observers (control: $5\male$, $3\female$, 108.2 ± 5.1 g body weight; auditory/visual: $4\male$, $4\female$, 106.4 ± 5.7 g body weight; auditory only: $4\male$, $4\female$, 107.6 ± 5.4 g body weight). The experiments (control, auditory/visual, auditory only)

were conducted in random order to minimize impacts of sample order on results. All of the observers and performers involved were food deprived for six hours prior to each trial to increase motivation during the tests.

In the control experiments, a performer was allowed to search for the man-made caches and establish new caches (hereafter "performer-made caches") freely in an arena alone for five hours (0700 – 1200 hours) (Fig. 1). Then the performer was moved out and the arena was quickly reset by rebuilding the man-made caches, and cleaning out all of the performer-made caches and seed fragments (left by the performer). An observer was then introduced to search for the man-made caches for five hours (1300 – 1800 hours). Compared to the treatments (auditory/visual and auditory only, seed below), observers in the control experienced same conditions of cache-searching except they had no any prior knowledge as to the caches. Cache-searching time (seconds from an animal venturing outside the nest to digging out a cache, recorded by replaying the video), harvested (number of discovered caches), and fate of each harvested cache (eaten, scatter-hoarded, and larder-hoarded) were recorded. A 'harvested cache' was a seed was dug out by an observer, a 'scatter-hoarded seed' was a seed was dug out and then individually buried in the soil or put into a shelter box (≤ 3 seeds per site), while a 'larder-hoarded seed' was a seed was moved into a nest or shelter box and placed together with other seeds (> 3 seeds per site). Total hoarded seeds = # number of scatter-hoarded seeds + # number of larder-hoarded seeds. Seed harvest and fates can reflect behavioural strategies adopted by the subjects in the presence of conspecifics that provided different cues from cache-searching.

In the 'auditory/visual' treatment, a performer was searching for the man-made caches and establishing new caches freely in an arena while an observer was caged (L × W × H = 40 cm × 30 cm × 30 cm steel cage, with water) in the opposite corner of the nest and covered with a transparent plastic bag (Fig. 1). The events of cache-searching and hoarding by the performer could be clearly seen and heard by the observer. After five

hours of performance (0700 – 1200 hours), the performer was moved out. The observer was then covered for one hour (1200–1300 hours) using a black box and the arena was quickly reset as described above in the control. The observer was then allowed to search for the man-made caches alone for five hours (1300–1800 hours). Parameters were recorded as the same as those in the control.

In the 'auditory only' treatment, an observer was caged (L× W ×H = 40 cm × 30 cm × 30 cm steel cage, with water) in the opposite corner of the nest and covered with a black plastic bag when a performer was freely searching for the man-made caches and establishing new caches in the arena. The observer could hear but not see the performer's seed-searching and hoarding events during the test (Fig. 1). The experiment was replicated and parameters were recorded as described above in the control.

Performer-made cache-searching

The performer-made caches searching experiments were conducted in 2016. Animals used in these experiments also included four performers (2♂, 2♀, 104.6 ± 7.2 g body weight) and 24 observers (control: 5♂, 3♀, 105.3 ± 6.1 g body weight; auditory/visual: 4♂, 4♀, 103.6 ± 6.3 g body weight; auditory only: 4♂, 4♀, 104.2 ± 7.2 g body weight). Animal handling and experimental procedures were as the same as those in the experiments of man-made cache searching except that only the performer-made caches were kept in the arenas during the stage of cache-searching by observers. All of the caches could be located and tracked by the monitor in each test.

Data analysis

Statistical analyses were conducted using SPSS for Windows v. 20.0 (Chicago, USA). The Generalized Linear Model (GLM) was used to test the effects of treatment sex and their interaction on different response variables including cache-searching time, proportions of harvested and cache fates. The proportional response variables

were modeled with binomial distributions, while the cache-searching time was modeled with normal distribution and log-10 transformed if necessary. Multivariate ANOVA was used to test the main effects of treatment on each parameter in males and females separately, and LSD (Least Significant Difference) was included for pairwise comparison between treatments. The effect of sex of subject on each parameter was also analyzed using a two-tailed independent samples t-test within each treatment. The significance level was set at $P < 0.05$ for all the tests and mean $\pm$ SE was reported.

RESULTS

Man-made caches

Searching time for man-made caches was significantly different among treatments ($P < 0.001$) (Table 1). The animals spent less time locating man-made caches when they experienced seeing and/or hearing cache-searching events of conspecifics (all $P < 0.05$) (Fig. 2, Table 1). The proportions of seeds harvested ($P = 0.004$), scatter-hoarded ($P < 0.001$), larder-hoarded ($P < 0.001$) and total hoarded ($P = 0.014$) by observers were significantly affected by treatment (Table 1). The subjects harvested and hoarded more seeds when they had prior experiences of seeing and/or hearing conspecific's caching events, scatter-hoarded more seeds in the auditory/visual treatment, and larder-hoarded more seeds in the auditory only treatment than in the other treatments (Fig. 3A, Table 1). Both males and females spent less time locating man-made caches in the auditory/visual and auditory only treatments than in the control, but sexual differences were not detected both between and within treatments (all $P > 0.05$) (Table 1, Fig. 4A). Main effects of sex on seed fates were not detected except for scatter-hoarded seeds ($P = 0.003$), with males scatter-hoarded more seeds than females (Table 1). The proportions of seeds harvested ($F = 7.067$, df =2, $P = 0.012$, ANOVA), scatter-hoarded ($F = 10.395$, df =2, $P = 0.004$) and larder-hoarded ($F = 20.962$, df =2, $P < 0.001$) by observers were significantly

affected by treatment in males. Males increased total harvested seeds in the auditory/visual and auditory only treatments, increased larder-hoarded seeds and decreased scatter-hoarded seeds in the auditory only treatment. Females did not change their hoarding intensity apparently in the three treatments (all $P > 0.05$). Differences between sexes within each treatment was not detected in all parameters except that males scatter-hoarded more seeds than females in the auditory/visual treatment ($t = 2.461$, df = 6, $P = 0.049$, t-test).

Performer-made caches

Searching time for performer-made caches was significantly affected by treatment ($P < 0.001$) (Table 1). The animals spent less time locating performer-made caches in the treatments of auditory/visual and auditory only than in the control (all $P < 0.05$) (Fig. 2, Table 1). Proportions of all seed fates were significantly affected by treatment (all $P < 0.05$) with one exception of scatter-hoarded seeds ($P = 0.356$) (Table 1). The chipmunks harvested, larder-hoarded and total hoarded more seeds, and ate fewer seeds when they had prior experiences of seeing and/or hearing conspecific's caching events (Fig. 3B, Table 1). Main effect of sex was detected in total harvested seeds ($P = 0.03$), with males harvested more seeds than females. Searching time ($F = 17.931$, df =2, $P < 0.001$, ANOVA), proportions of seeds of harvested ($F = 3.748$, df =2, $P = 0.050$), eaten ($F = 4.273$, df =2, $P = 0.046$), and total hoarded ($F = 4.276$, df =2, $P = 0.046$) were significantly different among treatments in males, where they used less time in cache-locating, increased total harvesting and hoarding, and reduced eating in the auditory/visual treatment compared to the other two treatments (Fig. 4B). Significant differences among treatments were not found in all parameters in females (all $P > 0.05$). Compared to males, females used less time in locating performer-made caches in the auditory only treatment ($t = 3.435$, df = 6, $P = 0.013$, t-test) (Fig. 4B), and scatter-hoarded fewer seeds in the auditory/visual treatment ($t = 2.767$, df = 6, $P = 0.033$).

DISCUSSION

For the evolution of food-hoarding behaviour to occur, the ability to pilfer caches from others is as important as cache protection for individual animals to maximize fitness (Vander Wall 1990). Given the lack of studies on behaviour of potential pilferers utilizing information about cache owners, we used Siberian chipmunks to test if information of cache-searching and hoarding events of conspecific individuals can help pilferers improving cache-pilfering and hoarding intensity. We found that the experimental animals spent much less time locating caches, and harvested and hoarded more seeds when exposed to visual and/or auditory cues from the cache-searching events of conspecifics. These results suggest that both visual and/or auditory cues of others can help Siberian chipmunks improving cache-pilfering and hoarding intensity, supporting our prediction. The western scrub-jays, another model scatter-hoarding species, are also sensitive to conspecific competitor's hoarding events, where the birds are more likely to be successful at pilfering caches after observing caching events by conspecifics (Grodzinski *et al*. 2012). Similarly, this jay species is also sensitive to visual and auditory cues that may be used by a conspecific competitor to detect their caches, and consequently reduces these cues when they hoard food (Stulp *et al*. 2009). Gray squirrels can estimate site-specific risks of cache pilfering and regulate their hoarding behaviour to reduce the probability of cache pilferage after eavesdropping interspecific competitors' calls (blue jay) (Schmidt & Ostfeld 2008). Our observations are consistent with these studies, whereby food hoarders are sensitive to visual and/or auditory cues of both conspecific and interspecific individuals, and alter their hoarding strategies to reduce cache loss and / or improve cache pilfering. In the field, it is opportunistic for animals to watch or hear hoarder's cache events because hoarders try to hide food items in secret (Dally *et al*., 2006; Grodzinski & Clayton 2010). Animals need to trade off whether to spend time foraging/caching or to peek at others and then pilfer from them. In rodents, olfactory ability has been highlighted as a major cue in food-searching, cache-retrieving and

pilfering (e.g., Briggs & Vander Wall 2004; Hollander *et al*. 2012; Yi *et al*. 2016a), but only a few studies have focused on their responses to visual and auditory cues in food-hoarding (e.g., Schmidt & Ostfeld 2008; Stulp *et al*. 2009). Here, we are the first to report that visual and auditory cues of other individuals are also important in cache pilferage in rodents.

It is not surprising that rodents, especially diurnal species like Siberian chipmunks, are able to use visual cues to pilfer caches of others, although few cases have been reported. It is widely accepted that mammals and birds retrieve caches using spatial memory, providing them a recovery benefit over losses from potential pilferers (reviewed by Shettleworth 1995; Clayton 1998). The integrated memory of 'what-where-when' structure enables animals to make correct decision in cache retrieval (Clayton *et al*. 2001; Babb & Crystal 2006; Roberts 2006; Scheid *et al*. 2007). For example, Eurasian jays and western scrub-jays know the difference between cached perishable food (e.g., invertebrates) and non-perishable food (e.g., nuts), and then remember when and where the food types can be recovered (e.g., Clayton *et al*. 1996; Clayton & Dickinson 1998, 1999a, b; Clayton *et al*. 2001). Yi *et al*. (2016b) reported that Siberian chipmunks can remember their own caches and avoid retrieving these caches in subsequent caching activities. Similar to remembering their own caching activities, animals can also remember others' caching activities and subsequently use this observational spatial memory to improve cache pilferage. Food hoarders usually hoarded food in secret, cease or delay caching when in the presence of other individuals, and/or try to invalidate the information of their caches that pilferers have gained, indirectly indicating that pilferers have the ability to remember cache events of hoarders and use these pieces of information to find caches in the absence of the owners (reviewed by Dally *et al*. 2006; Grodzinski & Clayton 2010). In this study, the subjects spent less time locating and recaching caches after hearing and seeing cache-searching and hoarding events of others, suggesting that visual and/or auditory cues provided by other individuals can help Siberian chipmunks improve cache-pilfering. Similar

observations have been shown in several species of birds (e.g., Mexican jays, Pinyon jays, ravens, western scrub-jays) and primates (reviewed by Grodzinski & Clayton 2010), but not in rodents (but see Barkley & Jacobs 1998).

The ability of using auditory cues to protect and pilfer caches has been largely ignored in food-hoarding animals. Western scrub-jays cache much less food in the 'noisy' substrate (small pebbles) than in the 'quiet' substrate (soil) when their cache events are eavesdropped by a competitor (Stulp *et al*. 2009). Gray squirrels reduce cache value to decrease pilferage risks when they hear blue jays' calls (Schmidt & Ostfeld 2008). Rhesus monkeys (*Macaca mulatta*) know what others can and cannot hear and try to reduce auditory information when they find food and eat (Santos *et al*. 2006). These studies imply that auditory information is important in food protecting and pilfering in animals. In our experiment that provided auditory cues only, the subjects spent less time locating caches after hearing cache-searching and hoarding events of others, suggesting that auditory cues provided by others can help Siberian chipmunks improving cache pilfering from other individuals. As far as we know, this is the first report that rodents can pilfer caches from others relying on auditory cues alone.

The animals spent less time locating caches and hoarded more seeds in the auditory/visual treatment than in the auditory only treatment, especially when the animals searched for the performer-made caches (Fig. 3B). These results suggest that both seeing and hearing conspecifics are expected to be more advantageous than hearing alone with respect to encoding information about caching events of others. In the field, it is difficult to test each sense separately because animals usually integrate olfactory, auditory, and visual cues, along with spatial memory, when searching for food (Vander Wall 1990; Grodzinski & Clayton 2010).

The observers increased harvesting and hoarding intensity both in the auditory/visual and auditory only treatments, suggesting that the performers act as competitors to stimulate the observers' hoarding intensity. An

increase in harvesting and hoarding in response to competitors has been reported in many rodents and birds, representing a general adaptive response in sympatric rodents (Huang *et al*. 2011; Zhang *et al*. 2011, 2014; Dittel *et al*. 2017). Increasing hoarding would help animals control more resources and compensate for cache pilferage when they encounter unpredictable and ephemeral food resource (Vander Wall & Jenkins 2003; Dally *et al*. 2006). After the man-made caches were discovered, the observers increased scatter-hoarding intensity in the auditory/visual treatment as well as larder-hoarding intensity in the auditory only treatment. In contrast, when searching for performer-made caches, the observers ate less and larder hoarded more in both the auditory/visual and auditory only treatments (Fig. 3). These context dependent variations in behaviour suggest a certain degree of behavioural plasticity in rodents (Luo *et al*. 2014). Rapidly burying seeds around the source (scatter-hoarding) has advantages to control resources and avoid complete cache loss (rapid sequestering hypothesis, Jenkins & Peters 1992), whereas larder-hoarded seeds facilitate cache protection (Vander Wall 1990). Many rodents and birds adopt both strategies and shift from one to the other in a context dependent manner (Dally *et al*. 2006; Zhang *et al*. 2011, 2014; Luo *et al*. 2014).

In our study, a few parameters of cache-searching and hoarding were affected by sex of animals. For example, females located caches faster than males in auditory only treatment when they searched for performer-made caches, and they scatter-hoarded fewer seeds than males in the auditory/visual treatment. Generally, females need more food for reproduction and feeding offspring after over-wintering (Burns & van Horik 2007; Jenkins 2011). Thus, females of many rodent species tend to hoard more foods and are more sensitive to competitors than males (Barkley & Jacobs 2007; Zhang *et al*. 2011). Our results partially support this statement (e.g., searching time, but not hoarding intensity), and suggest that sexual effects of animals on cache-searching and hoarding are context dependent.

To the best of our knowledge, this is the first report in Siberian chipmunks, or any rodent species, that visual and/or auditory cues of others can help animals improving cache-pilfering and hoarding intensity, and this ability is context dependent. Because the background (e.g., trap sites, prior experience, and kin relationship) of the subjects was unclear, our observations need more tests. Further studies should be conducted on more species and in a natural setting to examine how rodents integrate visual, auditory and olfactory cues when they pilfer caches from others.

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Table 1 Statistical results of main effects of sex and treatment on each parameter and pairwise comparison

between treatments using GLM model. Treatments are C, Control; A/V, Auditory/visual; A, Auditory only.

Alpha was set at 0.05 for all the tests ($P < 0.05$). *, **, and *** are significant differences at $P < 0.05$, $P <$

0.01, and $P < 0.001$ separately.

Parameters	Sex	Treatment	C vs A/V	C vs A	A/V vs A
	(χ^2/P, df=1)	(χ^2/P, df=2)	(r/P, df=1)	(r/P, df=1)	(r/P, df=1)
Man-made cache					
Searching time	0.183 / 0.669	15.631 / < 0.001***	73.87 / 0.001**	78.38 / < 0.001***	4.51 / 0.840
Harvested	1.931 / 0.165	10.813 / 0.004**	-21.8018 / 0.005	-22.0838 / 0.004**	-0.2820 / 0.971
Eaten	0.409 / 0.523	1.483 / 0.476	-3.4111 / 0.581	4.1112 / 0.504	7.5224 / 0.224
Scatter-hoarded	8.67 / 0.003**	17.383 / < 0.001	-6.0516 / 0.243	14.9113 / 0.004**	20.9629 / < 0.001***
Larder-hoarded	2.478 / 0.115	20.988 / < 0.001***	10.5517 / 0.107	-19.0225 / 0.004**	-29.5742 / < 0.001***
Total hoarded	0.606 / 0.436	1.831 / 0.400	4.4976 / 0.480	-4.1125 / 0.516	-8.6101 / 0.176
Performer-made cache					
Searching time	0.004 / 0.951	25.305 / <0.001***	340.17 / <0.001***	267.00 / <0.001***	-73.17 / 0.305
Harvested	4.734 / 0.03*	15.559 / <0.001***	-21.4528 / <0.001***	-11.8300 / 0.029	9.6228 / 0.077
Eaten	0.009 / 0.926	19.521 / <0.001***	39.2651 / <0.001***	18.7950 / 0.034*	-20.4701 / 0.021*
Scatter-hoarded	0.042 / 0.837	2.067 / 0.356	-6.5458 / 0.416	5.0000 / 0.532	11.5458 / 0.152
Larder-hoarded	0.087 / 0.767	16.371 / <0.001***	-32.7168 / <0.001***	-23.7950 / 0.004**	8.9218 / 0.287
Total hoarded	0.009 / 0.926	19.521 / <0.001***	-39.2651 / <0.001***	-18.7950 / 0.034*	20.4701 / 0.021*

Figure caption

Fig. 1 Design of the experimental arenas. Three red bricks were used as visual signs to facilitate animals locating man-made caches.

Fig. 2 Searching times for man-made caches and performer-made caches in Siberian chipmunks in the experiments of control, auditory/visual and auditory only. Data are mean ± SE. Bars with different letters indicates significant difference between treatments ($P < 0.05$).

Fig. 3 Proportion of cache fates of man-made caches (A) and performer-made caches (B) harvested by Siberian chipmunks in the experiments of control, auditory/visual and auditory only. Data are mean ± SE. Bars with different letters indicates significant difference between treatments ($P < 0.05$).

Fig. 4 Search times of males and females for man-made caches (A) and performer-made caches (B) in Siberian chipmunks in the experiments of control, auditory/visual and auditory only. Data are mean ± SE. Bars with different letters indicates significant difference between treatments ($P < 0.05$) and bars with asterisks means significant difference within treatments (*, $P < 0.05$).
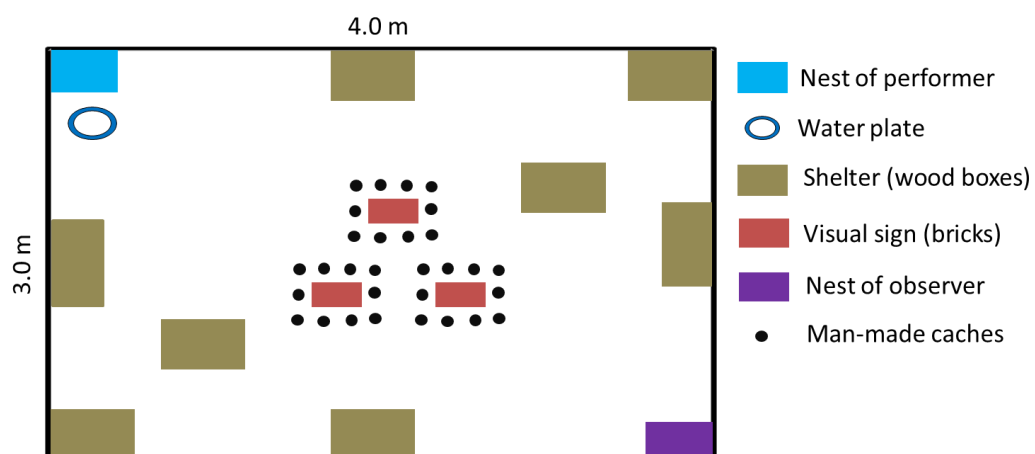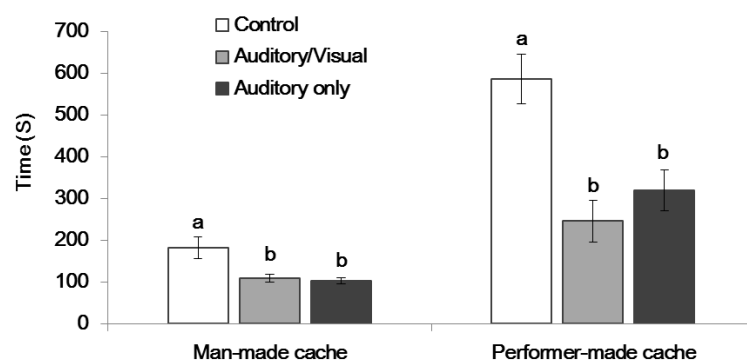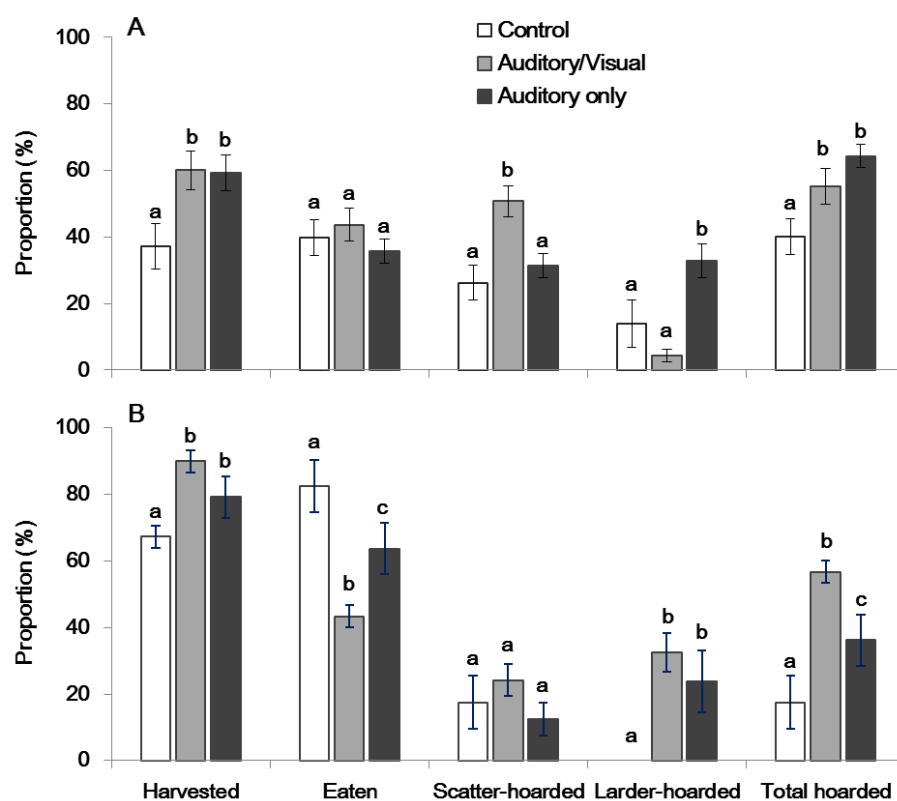
Fig. 1

4.0 m

3.0 m

Nest of performer
Water plate
Shelter (wood boxes)
Visual sign (bricks)
Nest of observer
Man-made caches

Fig. 2

Fig. 3

Fig.4