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Responses of a scatter-hoarding squirrel to conspecific pilfering: a test of the reciprocal pilferage hypothesis

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The reciprocal pilferage hypothesis argues that, despite the occurrence of pilferage, scatter-hoarding behaviour could evolve if cache loss is compensated by gains pilfered from others. However, this model has not been strictly tested because of the difficulty associated with tracking caches, including ownership, over long periods. Using infrared radiation cameras, we tracked caching of *Juglans regia* seeds by groups of two Père David's rock squirrels, *Sciurotamias davidianus*, within a large natural enclosure. Our goal was to quantify how squirrels responded to the presence of a conspecific when seed hoarding and pilfering and test the reciprocal pilferage hypothesis. We found that the numbers of seeds harvested from the seed sources and pilfered from conspecifics was initially low, increasing as seeds were removed and then dropping off once few seeds remained at the seed sources. Additionally, the number of seeds scatter hoarded increased with a decreasing number of seeds remaining at the sources. Seeds harvested from the source and pilfered from competitors were at first cached randomly within the enclosure and then centralized to the low-competition area near the nest as seed sources declined. Overall, pilferage was not high. The proportions of seeds pilfered did not vary between conspecifics and were positively correlated with each other over trials. More seeds were harvested from the seed sources than pilfered by competitors at the early stage of hoarding. These results suggest that, under conspecific competition, squirrels appeared first to compete for food at the sources, then for caches with each other as food sources decreased, and finally cache ownership became relatively stable. Squirrels compensated for cache loss by both harvesting food from the sources and pilfering caches from its competitor. The amount of seeds gained from pilfering was sufficient to replace pilfered caches, supporting the reciprocal pilferage hypothesis.

Food hoarding is an adaptive strategy in some animals (e.g. rodents and birds) in response to temporal variation in the availability of resources (Vander Wall, 1990). Food items can be hoarded in central larders (larder hoarding) or in multiple sites with a few food items in each (scatter hoarding) (Vander Wall, 1990). Larder-hoarding behaviour leads to aggressive cache defence where individuals exclude most thieves but are at risk of complete food loss from a superior competitor (Dally, Clayton, & Emery, 2006; Gerhardt, 2005). In contrast, scatter hoarding helps prevent complete cache loss by spreading out the cached items across space but increases costs associated with caching and later retrieving numerous caches (MacDonald, 1997; Preston & Jacobs, 2001). Many animals exhibit both types of caching strategies, and which strategy is used may depend on local conditions (Spritzer & Brazeau, 2003; Zhang, Wang, & Zhang, 2011, Zhang, Gao et al., 2014). Some species of rodents and birds scatter-hoard seeds into the soil and compete for these caches over a long period, thus making seed-hoarding behaviour an ideal model for studying food hoarding in animals (Thayer & Vander Wall, 2005; Vander Wall, 1990).

Cache pilferage from conspecifics and heterospecifics is one of the selective forces on the evolution of food-hoarding behaviour (Clarke & Kramer, 1994; Dally et al., 2006; Vander Wall & Jenkins, 2003). Generally, scatter-hoarders are sensitive to competitors when caching food items and tend to reduce cache loss by increasing hoarding, spacing caches, caching repeatedly, shifting to

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larder hoarding, evicting competitors and/or engaging in deceptive behaviour (pilferage avoidance hypothesis; Vander Wall & Jenkins, 2003; Dally et al., 2006; Steele et al., 2008, 2014). Andersson and Krebs (1978) and Stapanian and Smith (1978) proposed that food hoarding would become evolutionarily stable only if the hoarder gains significantly more from retrieving its own caches than a pilferer. Nevertheless, cache loss caused by pilferage is extremely high (up to 95% in 24 h) in some rodents and birds (Dally et al., 2006; Steele et al., 2015; Vander Wall & Jenkins, 2003) and how scatter-hoarders can store foods for long periods of times while sustaining such high amounts of pilferage has not been reconciled (Dally et al., 2006).

Several models have been proposed to explain the evolution of scatter hoarding when conspecific cache pilferage is high. One model specific to group-living hoarders such as tits and chickadees posits that caching behaviour evolves in population in situations of high conspecific pilferage because hoarders are better at cache recovery than nonhoarders during a period of food scarcity (Smulders, 1998). Some observations partially support this model because it has been found that scatter-hoarders are better at cache pilfering and gain more from their own caches in long-term hoarding than larder-hoarders, nonhoarders and/or pilferers (Dittel, Perea, & Vander Wall, 2017; Gu, Zhao, & Zhang, 2017; Wang et al., 2018; Zhang, Gao et al., 2014). The second model emphasizes kin selection of hoarders and posits that caching behaviour evolves in populations when pilferage is high if lost caches are being shared with related individuals, indirectly improving the fitness of the hoarder (Rothstein, 1980). Kin selection appears to promote cache sharing within the social group and has been observed in a few taxa that live in family groups (e.g. *Melanerpes formicivorus* and *Castor canadensis*; Novakowski, 1967; Koenig & Mumme, 1987).

The reciprocal pilferage model proposed by Vander Wall and Jenkins (2003) has attracted much attention in behavioural ecology. This model explains how solitary rodents with overlapping home ranges could survive high rates of pilferage without actively defending caches (Vander Wall & Jenkins, 2003). The authors argued that scatter-hoarding behaviour could evolve in the long term as long as the number of caches lost by a hoarder is replaced by pilfering from others, that is, there would be a net-zero loss in caches. As a result, each individual would end up with some caches that it had not necessarily cached itself. Reciprocal pilferage has been observed between conspecifics and heterospecifics in a few sympatric rodent species (Vander Wall, 2000; Jansen et al., 2012; Dittel et al., 2017), but it has still not been fully accepted (Dally et al., 2006). For example, if pilferage between individuals were asymmetric, some individuals would gain more caches while others would have insufficient caches (Leaver & Daly, 2001; Dally et al., 2006; Vander Wall, Enders, & Waitman, 2009; Zhang, Gao et al., 2014; Penner & Devenport, 2011; Gu et al., 2017; Niu et al., 2020). It is unlikely in this scenario that scatter hoarding would evolve as it would be more beneficial for individuals to larder-hoard. The reciprocal pilferage model may also be vulnerable to exploitation by cheaters, that is, individuals that harvest caches but do not cache food themselves (Andersson & Krebs, 1978), which would also probably lead to selective pressures to larder-hoard. Actually, asymmetrical pilferage has been observed in many heterospecific hoarders, but in these studies the pilferer usually compensated by changing its hoarding strategy (i.e. larder hoarding; Zhang, Gao et al., 2014; Penner & Devenport, 2011; Dittel et al., 2017; Gu et al., 2017; Niu et al., 2020). To our knowledge, empirical evidence of the reciprocal pilferage hypothesis is rare because it is difficult to follow seed movements in nature and also establish links between caches and individuals in long-term hoarding (but see Jansen et al., 2012; Gu et al., 2017).

Père David's rock squirrel, *Sciurotamias davidianus*, is widely distributed across northern China where it is endemic (Lu & Zhang, 2008). This diurnal squirrel shows caching and recaching behaviours when harvesting large seeds (e.g. *Juglans regia*, *Juglans mandshurica*) both in the field and under enclosure conditions (Lu & Zhang, 2008; Zhang, Steele et al., 2014, Zhang, Chu, Zhang, & Wang, 2017). The squirrels live solitarily but have overlapping home ranges with neighbours and hoard seeds in the overlapped areas (Lu & Zhang, 2008; Zhang, Steele et al., 2014). Conspecific pilferage is potentially high in the field. In our previous studies, more than 80% of the squirrels' primary caches were recached or moved to other locations over a 3–5-day period; however, whether cache owners or pilferers moved the seeds was unknown (Zhang, Steele et al., 2014; Zhang et al., 2017). Thus, *S. davidianus* is a unique model for observing scatter-hoarding behaviour of animals under conspecific competition (Zhang, Steele et al., 2014).

In this study, we tracked seed-hoarding behaviour of 14 pairs of *S. davidianus* (subject versus competitor hereafter) under natural enclosure conditions to understand interactions between seeds and individuals mediated by conspecific competition. Movements of 50 tagged *J. regia* nuts (each comprising a single seed enclosed in a hard endocarp, referred to as seeds hereafter) handled by the squirrels were tracked using infrared radiation cameras during a 10-day period in each trial. By tracking daily changes of seeds handled by the subjects, we tested the following three hypotheses. First, the squirrels would compete for seed at the seed sources at the beginning of the trials, then they would begin to pilfer caches from each other as seed availability decreased at the seed sources, and finally cache pilfering would reach a relatively stable state where individuals pilfered at a rate near to the rate of cache loss. Second, the presence of competitors would result in spatial niche separation between subjects and competitors, meaning the subjects' caches would be centralized in the low-competition area of the enclosure (i.e. near their nest). Third, per the predictions of the reciprocal pilferage hypothesis, cache losses pilfered by competitors could be compensated by cache gains pilfered from the competitors.

METHODS

Study Site

All experiments were conducted at the Liyuanling field station in the Donglingshan Mountains, northwestern Beijing city, China (115°20'–115°35'E, 39°55'–40°05'N; 800–1400 m above sea level). The temperate continental monsoon climate causes large seasonal changes in temperature (average temperature -5.7 °C in January and 25.1 °C in July) and precipitation (600 mm annual average precipitation, 74% in summer and 2% in winter) in the study area, probably leading to high intensity of food hoarding in small rodents in preparation for cold winters (Zhang et al., 2015). The typical landcover (shrublands, secondary forests and abandoned farmlands) in the study area is undergoing early secondary succession after lying fallow due to logging and grazing prohibition since the 1990s (Zhang, Chen, & Zhang, 2008). A more detailed description of the study area can be found in our previous studies (Zhang et al., 2008, 2016, 2017).

Study Animals

Sciurotamias davidianus is widely distributed in secondary forests, shrublands, abandoned farmlands and farmlands near villages within the study area (Lu & Zhang, 2008). Squirrel populations vary yearly but there is no record of local extirpation during any given year in the study area (Lu & Zhang, 2008). The large size

(210.2 ± 7.3 mm body length, 222.1 ± 23.2 g body mass, $N = 26$) and strong jaw (0.51 ± 0.05 g masseter mass, $N = 17$) allow the squirrel exclusive accesses to large seeds that are high in nutrients and protected by hard coats (e.g. *J. regia*, 9.1 ± 1.7 g seed mass, 1.2 ± 0.3 mm endocarp thickness, 131.8 kJ per seed); therefore, this squirrel is critical in the regeneration of the large-seed plants in the study area (Zhang & Zhang, 2008; Zhang et al. 2015, 2017).

Squirrels were captured in the forests, shrubs and abandoned farmland near the field station, in the Wayao village (2.5 km from the station), and in the Xiaolongmen forest park (10 km from the station) using live traps (12 × 25 cm and 12 cm high steel cages) in the summer of 2016 and 2017. Three to five plots at each location were selected for trapping and were used in rotation. In each plot, 30–50 traps were placed 5–10 m apart along three to five transects (150–250 m long, 200–300 m apart) for a 3-day period. A wooden board was attached to the upside of each trap to protect animals from rain and direct sunlight. Traps were baited with fresh kernels of *J. regia*, fresh peanuts (supplementary food source) and fresh cucumbers or carrots (water source); additionally, dry leaves were provided in the traps as nesting material. The traps were set in the evening (1730–1900 hours), and checked at 0600–0700, 1200–1300 and 1900–2000 hours every day for 3 days. Captured animals were visually inspected to determine whether they were pregnant or lactating females or juveniles, in which case they were released immediately at the capture sites. All other captured animals (including the trap) were individually covered using a cloth bag and carefully transferred to the laboratory. Trapping was stopped when we had enough animals to conduct the experiment. After being weighed, sexed and individually numbered, the squirrels were housed individually in a wheel cage (100 × 120 cm and 100 cm high) and kept separate in three well-ventilated rooms according to their trapping location. The captivity conditions were maintained at an ambient temperature (18–25 °C), a late-summer photoperiod (14:10 h light: dark), ad libitum water and nest materials (cotton), and an ample supply of native seeds (e.g. *J. regia*) and peanuts. The details of trapping and captivity are the same as described in our previous studies (Lu & Zhang, 2008; Zhang & Zhang, 2008; Zhang, Steele et al., 2014, Zhang et al., 2016, 2017). After at least a full week of acclimatization to indoor conditions, healthy individuals (i.e. active, normal appetite and weight maintenance) were selected for experiments. After testing, all animals were released at the site of capture.

Enclosure

The enclosure (40 × 50 m; Fig. 1) was constructed in an open area at the field station and fully described in our previous study (Zhang, Steele et al., 2014). The brick walls of the enclosure were 30 cm thick, 150 cm high and 30 cm below the ground surface. The enclosure was covered with wire mesh (1.2 × 1.2 cm grid) to prevent animals from entering or escaping the enclosure. The wire mesh was supported by a framework of 130 vertical steel tubes (2.5 m in height) distributed evenly across a 10 × 13 m grid. Vegetation within the enclosure was dominated by annual herbs with about 50% ground cover, similar to those around the enclosure. A feeding station, where tagged seeds were presented, was established at the centre of the enclosure, and two nest stations were set in opposing corners of the enclosure (Fig. 1). Each nest was monitored using an infrared radiation camera (Ltl-5210A, Little Acorn Outdoors, Green Bay, WI, U.S.A., IR camera hereafter) to identify which animal used them. The cameras were set on video record mode (video size: 640 × 480; PIR sensitivity: high; video length: 30 s; trigger interval: 10 s; the same mode for other cameras). The enclosure was divided into four quadrants to generate a Cartesian coordinate system to map caches (x-axis = -25–25 m, y-axis = -20–20 m). The quarter with the subject's nest was set out as

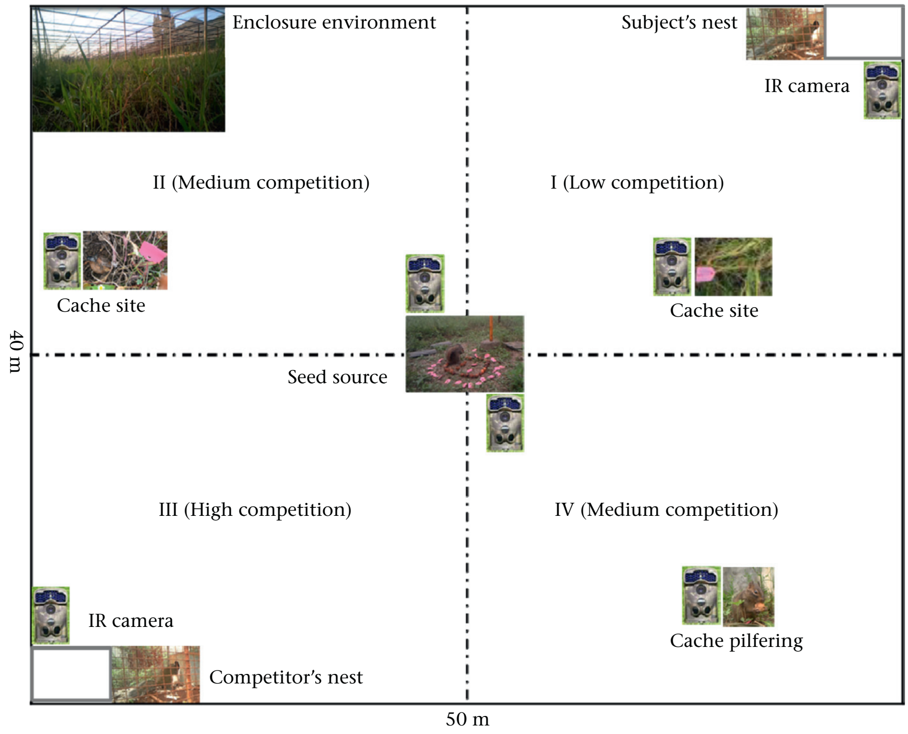

Figure 1. Design of the natural enclosure used in the seed-hoarding experiments with David's rock squirrels, *Sciurotamias davidianus*, under conspecific competition. Seed stations and nest stations were monitored, and caches were tracked using infrared radiation (IR) cameras. All photos were taken by these cameras during the experimental period. I, II, III, IV indicate the quadrant label within the enclosure.

quadrant I, the quarter containing the competitor's nest was quadrant III. Quadrant III was labelled as high competition, quadrant I as low competition and quadrants II and IV as medium competition (no nestboxes; Fig. 1).

Experimental Procedures

Experimental subjects (six females and eight males; mean ± SD body mass = 261.8 ± 19.8 g) were selected from the animals captured at the field station and competitors (nine females and five males; 261.6 ± 19.5 g) were selected from the individuals trapped at the Wayao village and the Xiaolongmen forest park to reduce kin effects. Subjects and competitors were paired (five pairs of ♂-♀, two pairs of ♀-♂, three pairs of ♂-♂ and four pairs of ♀-♀) for each trial. Body mass difference between each pair was less than 20 g to reduce the effects of social and physical dominance. Any effect of sex was not analysed because our previous observations showed that the competitor's sex had little effect on seed-hoarding behaviour in this squirrel species (Zhang, Steele et al., 2014). Competitors were marked on the tail tip using a spray hair dye (wine-red, patent No. 10-1017709, product No. J20151474, made in Korea) at least 7 days before testing (see Gu et al., 2017; Steele et al., 2008). Squirrels recovered from any handling stress within in a few hours and did not appear to exhibit any lasting effects in the subsequent experiments. In 2016 and 2017, nine and five subject and competitor pairs, respectively, were tested for a total of 14 trials.

The experimental seeds were bought from local residents. Seeds with visually similar sizes were used for testing; a random sample of 50 seeds were used to measure length (mean ± SD = 27.6 ± 2.3 mm), width (26.6 ± 2.1 mm) and mass (7.6 ± 1.4 g). Each seed was marked by tying a unique numbered plastic-tag (3.0 × 2.5 cm, 0.3 g) to the endocarp using a 5.0 cm piece of fine steel wire (revised from Zhang & Wang, 2001). Seeds moved by experimental animals could be easily relocated by searching for the tag within the enclosure. This method has been widely used in previous studies and shown to be effective at tracking rodent-dispersed seeds both in an enclosure and in the field (Gómez, Puerta-Piñero, & Schupp, 2008; Kempter, Nopp-Mayr, Hausleithner, & Gratzer, 2018; Xiao, Jansen, & Zhang, 2006). The tags may act as markers for cache pilferers both in the field and within the enclosure, but they do not result in higher cache pilferage than the other similar and widely used seed markers (e.g. thread, magnet, metal; Sork, 1984; Iida, 1996; Vander Wall & Joyner, 1998; Theimer, 2001; Xiao et al., 2006). Results from this study are unlikely to be affected by the seed tags because the presumed effects of tags on cache location were the same to subjects and competitors (also see Gu et al., 2017; Huang, Wang, Zhang, Wu, & Zhang, 2011; Niu et al., 2020).

During each trial, each subject and competitor pair were kept in the enclosure for 11 days until there was no significant change in the number of seeds they handled. On the first day they were allowed to acclimate to the enclosure conditions and to become accustomed to each other. Both subject and competitor could freely compete for seeds before and after caching. Squirrels (including their nest cages and water bottles) were introduced into the enclosure at 1200 hours on the first day. Fifty tagged seeds were provided on the second day and checked daily thereafter between 1200 and 1400 hours to map and monitor caches and record incidents of nut consumption (recorded as day 1, day 2, …, day 10). Some peanuts (8–10 g) were provided at the seed station on each day as supplementary food and to enable visual identification of the squirrel during visits. The seed station and each cache site were monitored with IR cameras (30–100 cm above the ground surface, ca. 100 m^2 scan area) to track the squirrels' movements of seeds in each trial (Fig. 1). Seed movement was tracked via the cache map and individual seed–squirrel interactions from the videos. Nitrile gloves were always worn when handling seeds to reduce any influence of human body odour on seed detection. Following each trial, the squirrels were released at the location they were captured, the enclosure was cleared of all seeds and seed fragments, and the nests were replaced. To limit any effect of the previous trial we had a 1-day break before reusing the enclosure.

During the trial, seed status was recorded as one of three categories (Zhang, Steele et al., 2014): (1) intact in situ (IIS), when a seed was intact at the original seed station; (2) eaten (E), when a seed was eaten and the seed tag and endocarp fragments were discarded on the ground; and (3) scatter hoarded (SH), when a seed was cached in the soil with the tag left on the surface.

Data Analysis

The behaviour of squirrels labelled subjects was used for analysis. The following parameters on day_i ($i = 1, 2, 3, \ldots, 10$) were calculated. (1) Percentage of seed remains at the source = seeds of IIS_i/total released seeds at the source (50 seeds) × 100. (2) Seed gain (G_i) or total harvested (TH_i) = harvested from the seed source (HfS_i) + pilfered from competitor (PfC_i) + remains of the day before ($\mathrm{R}_{i\text{-}1}$). (3) Seed loss (L_i) = eaten (E_i) + pilfered by competitor (PbC_i). (4) Seed remains (R_i) or total scatter hoarded (SH_i) = G_i–L_i. (5) Percentage of HfS_i (PfC_i, E_i, PbC_i, SH_i) = HfS_i (PfC_i, E_i, PbC_i, SH_i)/G_i × 100. (6) Percentage of HfS_i (PfC_i, SH_i) cached in a given area of the enclosure (low-, medium- and high-competition area) = HfS_i (PfC_i, SH_i)/area of a given area × 100.

Changes in HfS, PfC, E and SH over trial days were analysed to observe the behavioural responses of subjects to conspecific competition. Differences between PfC and PbC, HfS and PbC, and TH and PbC were analysed separately to observe whether squirrels compensated for conspecific pilferage by pilfering from competitors, harvesting from the seed sources, or both. The distributions of seeds in HfS, PfC and total SH categories for each area of the enclosure were analysed to observe the spatial responses of subjects when seed hoarding in response to conspecific competition.

Seed numbers and/or percentages (mean ± SE) were analysed with SPSS v20.0 (SPSS, Chicago, IL, U.S.A.). We combined data from males and females in each analysis to increase sample size because the sexes did not differ significantly in any of the tested variables (nonparametric tests of two independent samples of the Mann–Whitney *U* test). Normality of count data was tested by the Shapiro–Wilk test and log ($x + 1$) transformed to achieve normality when it was significantly different from normality (Chang & Zhang, 2011). Proportion data were modelled with binomial distributions and log-10 transformed, if necessary, to achieve normality. Nonparametric tests were used if normality could not be achieved with these data transformations. A generalized linear model was used to test whether each seed status (IIS, HfS, PfC, E and SH) and relative abundance of HfS, PfC and SH seeds in each area of the enclosure (low-, medium- and high-competition areas) changed significantly over trial days. Curve estimation regression analysis was used to find the best-fit curve for how these variables changed over time. Linear, quadratic, cubic and exponential models were run in curve estimation regression analysis and the significant model ($P < 0.05$) with the highest R^2 was selected. Spearman correlation was used to test the relationship between the seeds of PfC versus PbC, HfS versus PbC, and TH versus PbC separately, and a nonparametric two related-samples test was used to test the differences between each of the three pairwise variables on each trial day. A chi-square test was used to test whether the seeds of HfS, PfC and SH (seed number) were randomly hoarded in quadrants within the enclosure on each trial day. All statistical tests were two tailed, and differences were significant when $P < 0.05$.

Ethical Note

Animal handling in the experiments was supervised by the local governments and the Animal Ethical and Welfare Committee of the Central China Normal University (permission: SYXK(è)2015-0052), and was in accordance with the guide to ethical information required for *Animal Behaviour* papers. The squirrels' welfare was monitored throughout the experiments and individuals with any health problems (e.g. being inactive) were released at the location where they were captured.

RESULTS

Seed Fate

Seeds in the categories intact in situ (IIS; $\chi^2_9 = 60.072$, $P < 0.001$), pilfered from competitor (PfC; $\chi^2_9 = 17.552$, $P = 0.041$), harvested from the seed source (HfS; $\chi^2_9 = 36.934$, $P < 0.001$) and scatter hoarded (SH; $\chi^2_9 = 47.617$, $P < 0.001$) were significantly affected by experimental time (days), whereas eaten seeds (E) did not change significantly over time ($\chi^2_9 = 11.125$, $P = 0.267$). With the decrease in seeds at the seed sources (i.e. IIS seeds), HfS ($R^2 = 0.920$, $F_{3,\ 6} = 23.137$, $P = 0.001$) and PfC ($R^2 = 0.783$, $F_{3,\ 6} = 7.228$, $P = 0.020$) seeds changed in a bell-curve fashion and SH increased linearly ($R^2 = 0.977$, $F_{3,\ 6} = 145.883$, $P < 0.001$), but E did not change significantly ($R^2 = 0.536$, $F_{2,\ 7} = 4.051$, $P = 0.068$) over time (Fig. 2). The relationship between IIS and HfS was positive ($r_S = 0.903$, $N = 10$, $P < 0.001$) and that between IIS and SH was negative ($r_S = -0.827$, $N = 10$, $P = 0.003$; Fig. 2a, d).

Cache Distribution

During the first few days of testing, subjects randomly hoarded the seeds harvested from the seed source (HfS) within the enclosure; however, as seed availability decreased at the seed source subjects hoarded more HfS seeds in the low-competition area (i.e. near their nest) than other areas (Fig. 3a). Chi-square tests showed that cache distributions of HfS seeds were significantly different on day 5 ($\chi^2_2 = 19.312$, $P = 0.008$), day 6 ($\chi^2_2 = 12.464$, $P = 0.01$), day 7 ($\chi^2_2 = 9.341$, $P = 0.035$) and day 8 ($\chi^2_2 = 12.718$, $P = 0.001$; Fig. 3a) than what would be expected if seeds were randomly cached. Over time, daily relative abundance of HfS seeds decreased linearly in the low-competition area ($R^2 = 0.492$, $F_{1,\ 8} = 7.750$, $P = 0.024$) and the medium-competition area ($R^2 = 0.681$, $F_{1,\ 8} = 17.054$, $P = 0.003$), but changed with a bell-curve shape in the high-competition area ($R^2 = 0.949$, $F_{3,\ 6} = 37.443$, $P < 0.001$).

The subjects tended to cache the seeds pilfered from competitors (PfC) in the medium- and high-competition areas of the enclosure during the first few days of testing, while in the late stages of testing, they cached PfC seeds in the low-competition area more than other areas (Fig. 3b). Chi-square tests showed that the differences in PfC seed distribution were significant on day 4 ($\chi^2_2 = 13.247$, $P = 0.006$), day 5 ($\chi^2_2 = 11.142$, $P = 0.007$), day 6 ($\chi^2_2 = 13.152$, $P = 0.002$), day 7 ($\chi^2_2 = 9.402$, $P = 0.024$), day 8 ($\chi^2_2 = 8.326$, $P = 0.031$) and day 9 ($\chi^2_2 = 8.527$, $P = 0.041$; Fig. 3b). Over time, daily relative abundance of PfC seeds changed in a bell-curve fashion in the medium-competition area ($R^2 = 0.749$, $F_{2,\ 7} = 10.470$, $P = 0.008$) and the high-competition area ($R^2 = 0.797$, $F_{2,\ 7} = 13.750$, $P = 0.004$), but did not change significantly in the low-competition area (all $P > 0.05$).

Distributions of scatter-hoarded seeds (SH) were significantly different at the late stages of the trial, with more seeds in the low-competition area than elsewhere on day 6 ($\chi^2_2 = 6.357$, $P = 0.048$), day 7 ($\chi^2_2 = 11.440$, $P = 0.009$), day 8 ($\chi^2_2 = 10.734$, $P = 0.008$), day 9 ($\chi^2_2 = 14.217$, $P = 0.003$) and day 10 ($\chi^2_2 = 21.372$, $P < 0.001$; Fig. 3c). Daily relative abundance of SH seeds changed with a bell-curve shape in the medium-competition area ($R^2 = 0.894$, $F_{3,\ 6} = 16.804$, $P = 0.003$) and the high-competition area ($R^2 = 0.872$, $F_{3,\ 6} = 13.682$, $P = 0.004$) and increased linearly in the low-competition area ($R^2 = 0.794$, $F_{1,\ 8} = 30.754$, $P = 0.001$) over time.

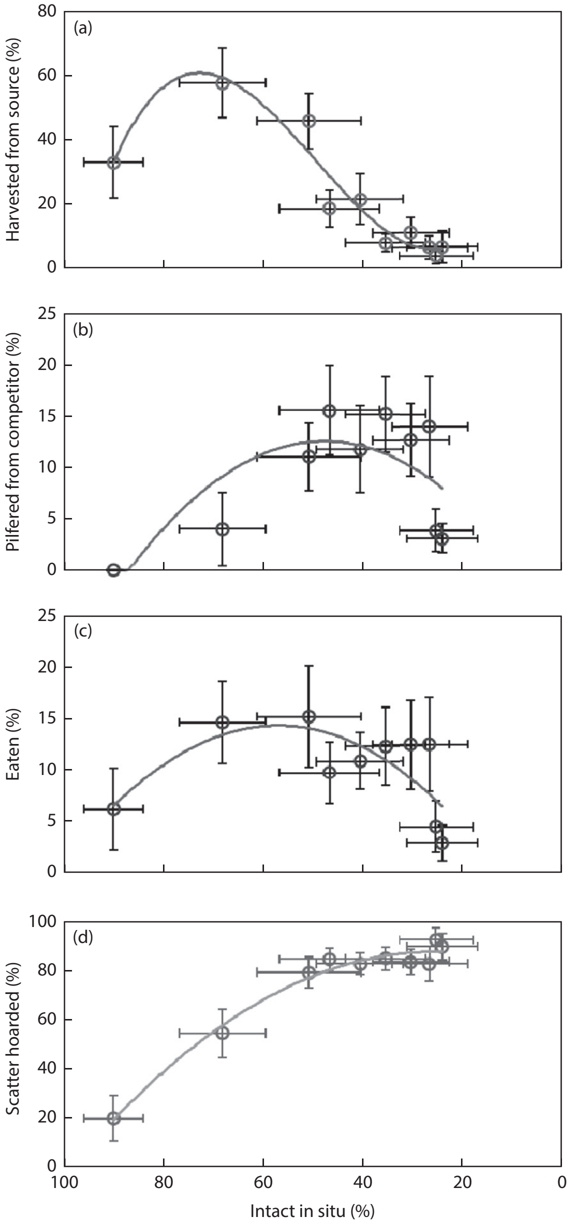

Figure 2. Relationship between the fate of each seed handled by squirrels and seed abundance at the seed sources (intact in situ) with a conspecific competitor present. (a) Harvested from the seed sources, (b) pilfered from the competitor, (c) eaten and (d) scatter hoarded. Percentage data are mean ± SE, $N = 14$.

Cache Pilferage and Compensation

The daily rate of pilferage between the squirrels was 0–15.8%. Seed pilferage by competitors (PbC) changed in a bell-curve fashion over time ($R^2 = 0.779$, $F_{2,\ 7} = 12.302$, $P = 0.005$). Seeds pilfered from competitors (PfC) were positively correlated with PbC ($r_S = 0.690$, $N = 10$, $P = 0.027$), and they had a linear relationship ($R^2 = 0.477$, $F_{1,\ 8} = 7.294$, $P = 0.027$). There were no differences between PfC and PbC on each trial day, with the exception that

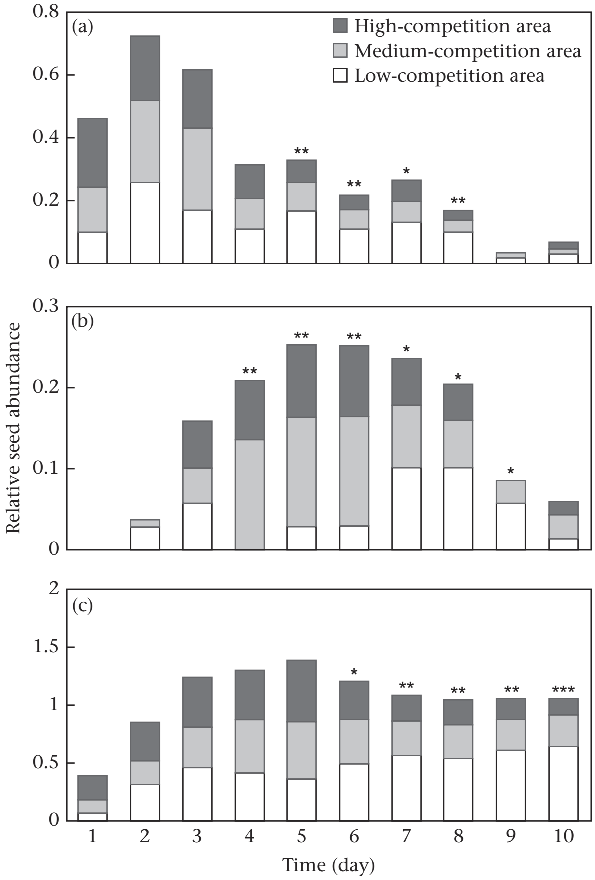

Figure 3. Dynamics of the distribution of caches made by squirrels within the enclosure over the trial with a conspecific competitor present. (a) Harvested from the seed sources, (b) pilfered from the competitor and (c) total scatter hoarded. The high-competition area was closest to the competitor's nest, the low-competition area was closest to the subject's nest and the remainder of the enclosure was a medium-competition area (see Fig. 1). Asterisks indicate significant differences in seed distribution between areas on a given trial day analysed by the chi-square test: *$P < 0.05$; **$P < 0.01$; *** $P < 0.001$. Data are mean relative seed abundance within each competitive area (seed number/area × 100).

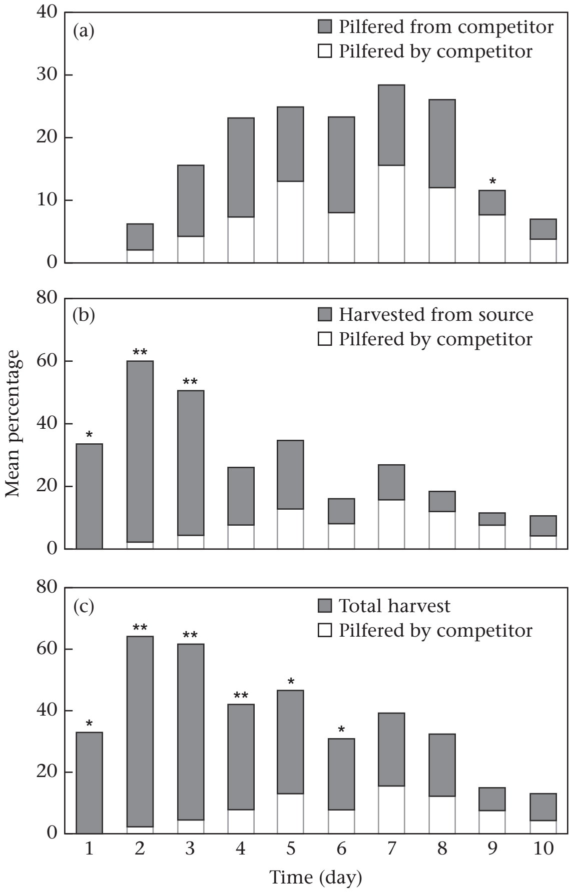

Figure 4. Compensation for conspecific pilferage in squirrels on each trial day within the enclosure. (a) Comparison between seeds pilfered from and by a competitor, (b) comparison between seeds harvested from the seed source and pilfered by a competitor and (c) comparison between total harvested seeds and seeds pilfered by a competitor. Asterisks indicate significant differences in seeds between each pair on a given trial day: *$P < 0.05$; **$P < 0.01$.

there were fewer PfC seeds than PbC seeds on day 9 ($Z = -2.032$, $P = 0.042$; Fig. 4a).

There were more seeds harvested from the seed source (HfS) than PbC seeds in the early stages of trials (day 1: $Z = 2.214$, $P = 0.027$; day 2: $Z = 2.963$, $P = 0.003$; day 3: $Z = 2.907$, $P = 0.004$), and they did not differ from each other in the later stages (Fig. 4b). PbC seeds tended to increase as HfS seeds decreased ($Z = -0.559$, $P = 0.093$), and this change was marginally linear ($R^2 = 0.313$, $F_{1,8} = 3.640$, $P = 0.083$).

There were more total harvested seeds than PbC seeds on day 1 to day 6 (day 1: $Z = 2.214$, $P = 0.027$; day 2: $Z = 2.986$, $P = 0.003$; day 3: $Z = 2.987$, $P = 0.003$; day 4: $Z = 2.904$, $P = 0.004$; day 5: $Z = 2.040$, $P = 0.041$; day 6: $Z = 2.223$, $P = 0.026$; Fig. 4c). Overall, PbC seeds had a negative relationship with total harvested seeds ($Z = -0.361$, $P = 0.306$), but this was not significant (all $P > 0.05$).

DISCUSSION

Under intensive competition from conspecific individuals, food-hoarding animals have to consider how to compete for food at the food sources, what to do with harvested food (e.g. eat or hoard), and how to protect the food they cache (Dally et al., 2006; Grodzinski & Clayton, 2010; Vander Wall, 1990; Vander Wall & Jenkins, 2003). Our results showed that, under conspecific competition, seeds harvested from the seed sources and seeds pilfered from competitors changed in a bell-curve fashion, with the number of seeds scatter hoarded initially increasing as the number of seeds available at the seed sources decreased (Fig. 2). Pilferage between the subject and competitor was not high initially, but increased over time until finally reaching an equilibrium (Figs. 2b and 4a). Whether the seeds were harvested from the seed sources or pilfered from the competitor, subjects were likely to cache them randomly within the enclosure during the first few days of testing. As seeds became less available at the seed sources in the late stages of testing, subjects preferred to cache seeds in the low-competition area (i.e. near the nest; Fig. 3). These results support the predictions of hypotheses 1 and 2, that squirrels should initially compete for food at the seed sources at the early stage of hoarding, then subsequently compete with each other for caches (i.e. reciprocal pilfering) when seed availability is reduced at the sources and eventually stabilize (cache lost = cache gain). In accordance with the predictions of hypothesis 3, seeds pilfered from competitors were positively correlated with seeds pilfered by competitors and did not differ over time, supporting the reciprocal pilferage hypothesis (Fig. 4a). Significantly more seeds were harvested from the seed sources and pilfered from competitors than pilfered by competitors at the early stage of hoarding, suggesting that the squirrels compensated for cache loss by both harvesting from the food sources and pilfering from others (Fig. 4b and c).

Behavioural Responses to Conspecific Competition

Our results showed that the squirrels initially harvested seeds from the sources, rapidly hoarded them near the sources, and then subsequently recached these seeds to relatively secure places (i.e. the nest areas) as seeds became scarcer at the sources (Figs. 2 and 3). These results are consistent with our previous studies on *S. davidianus* dispersing *J. mandshurica* nuts under similar conditions in an enclosure and in the field (Zhang, Steele et al., 2014). Under the pressures of conspecific competition (where competitors were restricted to cages), the squirrels initially cached seeds near seed sources and then subsequently cached at more secure places in the same direction (e.g. nest areas, under shrubs) at lower densities (Zhang, Steele et al., 2014). Observations of our experimental squirrels suggest that scatter hoarding is a dynamic process driven by multiple factors (Dally et al., 2006). For example, pilferage pressure drives hoarders to move caches repeatedly and space caches either further apart or out of sight to prevent pilferers from accessing them (pilferage avoidance model; Dally et al., 2006; Gálvez, Kranstauber, Kays, & Jansen, 2009; Vander Wall & Jenkins, 2003 and the spacing of caches represents a trade-off between the benefits of pilferage reduction and the costs of cache retrieval (optimal density model; Clarkson, Eden, Sutherland, & Houston, 1986; Stapanian & Smith, 1978). Our results on rapid scatter hoarding of seeds close to the source and then subsequent transfer to caches in burrows or core areas of the home range are best explained by the rapid sequestering hypothesis (but not mutually exclusive with the pilferage avoidance model; Clarkson et al., 1986; Jenkins & Peters, 1992; Jenkins, Rothstein, & Green, 1995; Stapanian & Smith, 1978). This model proposes that animals rapidly scatter-hoard seeds around the sources to maximize food harvest, and recache seeds to more secure places to minimize pilferage and allow for long-term storage (Jenkins & Peters, 1992). Rapidly sequestering seeds is thought to be an evolutionary strategy adopted by granivores (e.g. *Tamias striatus*, *Tamias amoenus*, *Dasyprocta punctata*, *Dipodomys ordii*) in response to ephemeral pulses of seed production in many ecosystems (e.g. temperate forests; Leaver, Hopewell, Caldwell, & Mallarky, 2007; Moore et al., 2007; Hopewell, Leaver, & Lea, 2008; Gálvez et al., 2009; White & Geluso, 2012; Zhang et al., 2017). For example, artificially released seeds (e.g. *Quercus wutaishanica, Armeniaca sibirica, J. mandshurica* and *Amygdalus davidiana*) were harvested and repeatedly cached (two to seven times) increasingly further from the seed sources over time by small rodents (e.g. *Apodemus peninsulae*, *Niviventer confucianus*, *S. davidianus*, *Tscherskia triton* and *Tamias sibiricus*) in a few days in seed-poor years in our study area (Zhang et al. 2015, 2016, 2017). However, this behaviour is not clearly understood in most studies because it is extremely difficult to follow the fate of individual caches in the field. Here, we have provided evidence of rapid seed sequestering in *S. davidianus* based on individual seed–squirrel interactions during a 10-day period of seed hoarding.

An increase in caching in response to food competition and/or pilferage has been reported in some mammals and birds (e.g. *Garrulus glandarius*, *Peromyscus leucopus*, *Aphelocoma californica*, *A. peninsulae*, *N. confucianus*, *Sciurus carolinensis*; Dally et al., 2006; Hopewell et al., 2008; Luo et al., 2014; Vander Wall & Jenkins, 2003), and might be a general adaptive response in sympatric rodents (Huang et al., 2011; Luo et al., 2014). In this study, the squirrels continuously increased scatter hoarding in response to conspecific competition, supporting previous studies and implying that animals are expected to increase hoarding to control more food when the resources are ephemeral (Jenkins & Peters, 1992). However, increased hoarding is potentially challenging, or even impossible, for animals when resources are limited, because food gains under such conditions would be too few to offset the costs of harvesting said food (Dally et al., 2006). An alternative option is moving the temporarily hoarded seeds to more secure places (e.g. in burrows) for larder hoarding. Our results showed that the squirrels appeared to hoard more seeds near the nest area of the enclosure, but did not shift from scatter hoarding to larder hoarding over the trial, which was partially congruous with some previous studies in rodents (Luo et al., 2014; Niu et al., 2020; Spritzer & Brazeau, 2003). Alternating between scatter and larder hoarding reflects a trade-off between reducing catastrophic loss and facilitating cache defence (Dally et al., 2006; Luo et al., 2014). The squirrels utilized scatter hoarding to rapidly sequester resources in response to conspecific competition (Jenkins & Peters, 1992). The lack of larder hoarding in both this and our previous study (Zhang, Steele et al., 2014) may be due to limited space and too few suitable caching sites in the enclosure. In the field, the squirrels would cache seeds (e.g. *A. sibirica*, *J. mandshurica*, *A. davidiana* and *J. regia*) within their home ranges and finally transfer these seeds into burrows for larder hoarding and consumption, as evidenced by piles of endocarp fragments of seeds at the entrances of their burrows in the field (H.M. Zhang, personal observations).

Cache Pilferage and Compensation

Caches pilfered from competitors were positively correlated with those pilfered by competitors and they offset each other (Fig. 4a), supporting the reciprocal pilferage hypothesis (Vander Wall & Jenkins, 2003). Although reciprocal pilferage has been observed in populations and communities of some rodent species, evidence for this model is still scarce owing to the uncertain nature of individual interactions among animals in these examples (Dittel et al., 2017; Niu et al., 2020; but see Gu et al., 2017). The model is specific to asocial animals that share home ranges, hoard and pilfer foods, and suffer from a high pressure of pilferage (Vander Wall & Jenkins, 2003). However, few of the subjects and conditions of previous studies were a total match to the initial requirements for the model (e.g. Dittel et al., 2017; Gu et al., 2017; Penner & Devenport, 2011; Price & Mittler, 2003). In contrast, we conducted the present study on *S. davidianus* within a large enclosure and established the individual pilferage interactions of squirrels during a 10-day period. The results provided evidence for the reciprocal pilferage hypothesis. Despite our results, cache loss may be difficult to replace via pilfering in natural settings because competition/pilferage happens among conspecifics and heterospecifics that have different hoarding strategies and pilferage abilities (Dittel et al., 2017; Gu et al., 2017; Zhang, Steele et al., 2014). As a result, pilferage between animals can be asymmetrical, whereby some species may have advantages over others (Gu et al., 2017; Leaver & Daly, 2001; Penner & Devenport, 2011; Vander Wall et al., 2009; Zhang, Gao et al., 2014). Based on the individual interactions between rodents and seeds in a subtropical forest in southwestern China, a field study of seed caching and pilferage among sympatric rodent species showed that seed-hoarders have an advantage over pilferers in recovering cached seeds (Gu et al., 2017). Other studies show that scatter-hoarders are better cache pilferers than larder-hoarders (Dittel et al., 2017; Vander Wall et al., 2009; Wang et al., 2018; Zhang, Gao et al., 2014). Thus, the reciprocal pilferage hypothesis needs to be studied more in communities that have multiple species of seed-caching animals.

Our results also showed that the experimental squirrels tended to compete for resources from the seed sources, rather than pilfer from the competitors, as evidenced by the fact that significantly more seeds were harvested from the seed sources than pilfered from the competitors (Fig. 4b and c). The pilferage ratios changed in a bell-curve fashion and reached a relatively low and stable level at the late stage of the 10-day test period, suggesting that cache pilferage between hoarders may not be very high once seed sources are diminished after the initial resource pulse. Thus, more studies are needed using multiple species and resources to test food pilferage and compensation between long-term hoarding animals.

Author Contributions

H.Z. and Z.W. designed the study, Z.W., G.H. and C.P. conducted the enclosure experiments and H.N., H.Z. and Z.Z. wrote and revised the manuscript.

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