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Scatter-hoarding behavior in Siberian chipmunks (*Tamias sibiricus*): An examination of four hypotheses

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ABSTRACT

To store food items, animals employ scatter-hoarding, larder-hoarding, or a combination of both. However, little is known about the factors that drive animals to use different strategies. In the present study, we used seed placement experiments, both in the field and in semi-natural enclosures, in order to test four hypotheses related to the scatter-hoarding behavior of the Siberian chipmunk *Tamias sibiricus*. To investigate whether scatter-hoarding is a vestigial non-adaptive behavior (non-adaptive hypothesis), we provided each of 23 Siberian chipmunks with 30 tagged intact *Quercus mongolica* acorns, which were placed at the center of their enclosures, and then observed their behavior. To test whether scatter-hoarding behavior is a response to insufficient larder space (lack-of-space hypothesis), we provided each of 14 Siberian chipmunks with 30 tagged intact acorns, with open artificial burrows and then closed artificial burrows. To determine whether scatter-hoarding was used as a means to rapidly sequester food items from food patches (rapid-sequestering hypothesis) and whether the distance between food patches and burrows affects hoarding behavior, 10 chipmunks were randomly selected, and 30 marked acorns were introduced to their enclosures at 3.5, 0.5, and 7 m from their burrows, over a period of 3 days. To test whether scatter-hoarding represents a behavioral strategy to avoid the pilferage of food resources by competitors (pilfering-avoidance hypothesis), 10 randomly selected chipmunks were released into the enclosures immediately following acorn placement, and over the next few days, the other 10 rodents as potential pilferer were caged and put in the corner of the enclosures before acorn placement, with one individual in each enclosure. This deployment was expected to invoke anti-pilferage behavior in the focal caching animals. The results of the present study indicated that Siberian chipmunks exhibit scatter-hoarding behavior more often than larder-hoarding, regardless of age and sex. Scatter-hoarding behavior was common in Siberian chipmunks, thus failing to support the non-adaptive hypothesis. Meanwhile, the availability of larder space (open or closed burrows) had no significant effect on the intensities of either larder- or scatter-hoarding, thereby failing to support the lack-of-space hypothesis. In addition, the distance between seed sources and burrows also failed to influence the seed-hoarding behavior of the chipmunks, either in the field or in the semi-natural enclosures; and the chipmunks did not transfer scatter-hoarded acorns into dens. Therefore, we argue that the primary function of scatter-hoarding is not to ensure the rapid harvesting of *Q. mongolica* acorns, thereby failing to support the rapid-sequestering hypothesis. In contrast, Siberian chipmunks did increase scatter-hoarding behavior when faced with a risk of pilferage by superior competitors, which suggests that the scatter-hoarding strategy adopted by Siberian chipmunks can be explained by the pilfering-avoidance hypothesis, and the observation that the chipmunks intentionally moved seeds from their artificial burrows to scatter-hoard them further supports this hypothesis.

1. Introduction

Food hoarding is a wide-spread behavior adopted by various mammals, birds, and insects [1–3]. It is widely assumed that food hoarders store or cache food to cope with unpredictable variations in resource availabilities, inclement weather or risk of predation [1,4]. In addition, seed caching is widely accepted to be an economic strategy adopted by food hoarding animals and has important ecological consequences for plants whose seeds are harvested and stored [1,5].

Animals use two main strategies to store food items, scatter-hoarding and larder-hoarding [6]. Unlike larder-hoarding animals that deposit food at one or a few sites, scatter-hoarding animals usually store seeds in small, widely scattered, shallow caches [1,6,7], playing an important role in seedling recruitment. Despite this significance in the plant regeneration, the evolutionary basis of seed scatter-hoarding is poorly understood [8]. Although larder-hoarding is commonly found in food hoarding mammals [4], it has long been a puzzle why many groups of

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animals deploy the behavior of scatter-hoarding or use a combination of larder-hoarding and scatter-hoarding [9–11], because scatter-hoarding involves increased energy to establish small subsurface caches of food items in numerous locations [1,6], to remember each cache they made and then recover these caches [1,7,12], and/or to escape predation risks when making caches [13,14]. Four hypotheses have been put forward to explain the underlying mechanisms of scatter-hoarding behaviors of various animals. Yahner [15] found that scatter-hoarding is just a rare food-storing strategy appearing at random in any individual of eastern chipmunks, and then put forward the 'non-adaptive hypothesis' suggests. However, scatter-hoarding has been widely found in food caching animals and most of individuals in the population actively participate in scatter-hoarding [8,16], suggesting that scatter-hoarding is not a vestigial non-adaptive behavior pattern. Therefore, 'non-adaptive hypothesis' is incapable to account for the ubiquitous scatter-hoarding behavior of animals either at population or community levels. After investigating the food hoarding behaviors of red-tailed chipmunk and red squirrel, Lockner [17] and Hurly & Robertson [18] suggested that scatter-hoarding appears to be a behavioral response to lack of suitable larder space (i.e., 'lack of space hypothesis'). However, increasingly accumulated evidence shows that hoarding animals tend to scatter-hoard seeds even when provided with suitable and sufficient larders [8,19]. Based on the study on food hoarding behavior of cliff chipmunks, Hart [20] first proposed that scatter-hoarding represents a rapid harvesting of ephemeral food resource of in response to potential competitors (i.e., 'rapid-sequestering hypothesis'). Clarke & Kramer [8] propose that the advantage of rapid-sequestering by scatter-hoarders is partially due to a short travel distance to the hoarding sites, especially when the food source is far from the animal's burrow [21]. However, when faced to potential competitors, hoarding animals do not always increase scatter-hoarding activity [22,23]. If the function of scatter-hoarding is to sequester food from competitors for later use, hoarding animals are expected to rapidly sequester the food items by scatter-hoarding and then immediately transfer them into larders. However, little is known about this model, perhaps due to lack of effective approaches to investigate seed movement from scatter-hoards to larder-hoards [8,24]. As to the 'pilfering-avoidance hypothesis', it proposes that if animals are unable to defend their hoarded food, then an alternative strategy of scatter-hoarding will be adopted [1,4,25]. However, this hypothesis cannot explain why many groups of animals increase seed scatter-hoarding under extremely high level of pilferage [26]. Moreover, scatter-hoards can also be pilfered by inter- or intra-population competitors [1,9,14,27,28], making this hypothesis less effective. Therefore, much effort needs to be made to further explore the behavioral basis of scatter-hoarding of seed-storing animals.

Flexibility in food-hoarding patterns is most common in solitary rodents [6,9–11]. Not surprisingly, Siberian chipmunks mainly scatter-hoard various seed species in the northeast China, whereas occasionally larder-hoard a small portion of seeds in their burrows [16]. Although several hypotheses have been proposed to explain the scatter-hoarding of food hoarding animals [8], we have little knowledge of the behavioral basis of scatter-hoarding of Siberian chipmunks. Here, we deployed seed placement experiments in the semi-natural enclosures and field, in an attempt to test the four hypotheses related to scatter-hoarding behavior of Siberian chipmunks, i.e., 'non-adaptive hypothesis', 'lack of space hypothesis', 'rapid-sequestering hypothesis' and 'pilfering-avoidance hypothesis.'

2. Materials and methods

2.1. Study site and species

The study was conducted from September to November 2010 and 2011 in the Dongfanghong Forestry Center (mean elevation of 750 m, 45°58′N, 129°08′E) in the Dailing District, Yichun City, Heilongjiang Province, northeast China [29]. To trap *Apodemus peninsulae* and *Tamias sibiricus* for enclosure experiments, steel-framed live-traps (H × W × L = 9 cm × 10 cm × 25 cm), baited with peanuts and some carrots were placed in forests at 5 m intervals along four transects at 8: 00 am. While, large traps (H × W × L = 15 cm × 15 cm × 40 cm) baited with Korean pinecones and carrots were used to capture *Sciurus vulgaris*. All traps were pre-baited for 2 days and protected from predators by wrapping with steel mesh. Traps were checked twice daily in the early morning and late afternoon for 4 consecutive days. Bedding was provided in each trap. Water was not available but the carrots were expected to provide the water supply. The captured animals were transported by vehicle to the animal housing room within about 30 min. Trapping stopped when encountering bad weather like heavy rainfall days. *T. sibiricus* and *S. vulgaris* transported to the housing room were kept in steel frame cages (H × W × L = 90 cm × 40 cm × 50 cm) individually in condition of room temperature and natural photoperiod. They were provided with nests, carrots, peanuts, tree seeds and water ad libitum. No animals died during field trapping and laboratory procedures. In the enclosures, all animals were provided with several peanuts and water in addition to the experimental seeds. Following behavioral experiments, all animals were released at the original sites of capture after carefully checked by a veterinarian to ensure that they were in good condition and capable to survive the coming winter.

2.2. Experimental protocols

2.2.1. Establishment of enclosures

We conducted behavioral experiments in 16 separate semi-natural enclosures (10 m × 10 m) previously established in an open, non-forested area [16]. The enclosures were built using bricks about 2.5 m high above ground and 0.5 m below the soil surface. The walls were coated with cement to prevent climbing by the animals and the top of the enclosure was covered with plastic nets to prevent access by predators. An artificial burrow was provided at one corner of each enclosure, and an arena was established at the center of each enclosure.

2.2.2. Testing the non-adaptive hypothesis

To test if scatter-hoarding is a vestigial non-adaptive behavior pattern of Siberian chipmunks (testing 'non-adaptive hypothesis'), we provided each of 24 Siberian chipmunks (14 female, 10 male, body mass = 92.48 ± 2.66 g, one individual escaped was missing the experiments) with 30 tagged intact *Quercus mongolica* acorns at the center of the arena to determine caching preferences. Acorns were labeled using methods slightly modified from those reported by Yi & Zhang [29]. A minute hole (0.3 mm in diameter) was drilled at the basal end of each acorn, avoiding damage to the embryo. We slipped a 10 cm thin steel wire through the hole and fastened it to the acorn, and then attached a white flexible plastic tag (2.5 cm × 3.5 cm, <0.3 g) to the opposite end of the steel thread [16]. All animals were fed prior to seed placement in the enclosures, ensuring that the animals actually use the artificial burrows or dig dens as their larders. Each animal was released into one enclosure between 0700 h to 0800 h on the day of the experiment. Acorns were placed at the center of each enclosure and were the only food source available to the animals during the experimental trials. We checked the acorns at the end of each trial (1700 h). Seed fates were classified into six categories: 1) intact in situ (IS), 2) eaten in situ (EIS); 3) eaten after removal (EAR), 4) intact after removal (IAR); 5) cached after removal (CAR) and 6) larder-hoarded after removal (LAR). Based on the previous studies, we predicted that Siberian chipmunks will universally scatter-hoard more acorns than larder-hoard.

2.2.3. Testing the lack of space hypothesis

To test if scatter-hoarding behavior appears to be a response to lack of larder space (lack of space hypothesis), we randomly selected 14 Siberian chipmunks (8 female, 6 male, body mass = 95.62 ± 3.41 g). We firstly provided each Siberian chipmunk with 30 tagged intact