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Food-hoarding behaviour of David's rock squirrel *Sciurotamias davidianus* *

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Abstract Food storage is an important adaptation of some animal species to the temporal variation or unpredictable food supplies. David's rock squirrel *Sciurotamias davidianus* occurs in mountainous and hilly areas of north China. Food-hoarding behaviour of this species was unknown. We set up four semi-natural enclosures in the Donglingshan Mountain area near Beijing, and investigate the hoarding strategy of 12 David's rock squirrels and their response to perceived pilferage on seeds of walnuts *Juglans regia* and wild apricot *Prunus armeniaca*. The results show that: 1) David's rock squirrels hoarded food items in both larder and scatter patterns but more items were scatter hoarded; 2) when confronted by perceived pilferage on hoarded food, David's rock squirrels increased both larder hoarding and scattered hoarding; 3) none of the seeds of wild apricot and walnut were eaten at the feeder. David's rock squirrels consumed more seeds of wild apricot than that of walnuts outside nest boxes; 4) David's rock squirrels only scatter hoarded walnuts; and 5) seeds of walnuts were transported greater distances than that of wild apricot. The result suggests that David's rock squirrels might play different roles in natural regeneration of walnuts and wild apricots [*Acta Zoologica Sinica* 51 (3): 376-382, 2005].
Key words *Sciurotamias davidianus*, Food hoarding, Hoarding strategy, Pilferage, Food selection, China

岩松鼠的食物贮藏行为 *

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摘 要 食物贮藏是许多动物对不可预见的食物供应变化的一种重要适应。岩松鼠（*Sciurotamias davidianus*）为中国特有物种，广泛分布于华北地区的山地和丘陵地带。作者在北京市东灵山地区建造半自然围栏（4 m× 3 m× 1 m），以核桃（*Juglans regia*）和山杏（*Prunus armeniaca*）种子为备选食物，对岩松鼠（12 只）的食物贮藏行为进行了研究。数据的统计分析采用 SPSS for Windows 进行。研究结果表明：1）岩松鼠表现出集中和分散两种食物贮藏方式，而分散贮藏是其偏好的贮藏方式；2）当遇到贮藏食物被盗窃时，岩松鼠倾向于搬运更多的食物进行集中和分散贮藏；3）岩松鼠没有在食盘就地取食任何一种食物；把食物搬离后，岩松鼠所取食的山杏种子数量明显多于所取食的核桃数量；4）岩松鼠只选择核桃进行分散贮藏；5）岩松鼠对核桃的搬运距离大于山杏种子。本研究结果提示，在自然条件下，岩松鼠对核桃和山杏的天然更新起着不同的作用［动物学报 51 (3)：376-382，2005］。
关键词 岩松鼠 食物贮藏 贮藏策略 盗食 食物选择 中国

Hoarding food for later consumption is a common foraging tactic used by a wide variety of taxa. Food caches are distributed in a variety of ways, from highly clumped to highly dispersed. The extremes of

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this spectrum of cache-dispersion patterns have been termed larder hoarding and scatter hoarding (Smith and Reichman, 1984, reviewed by Vander Wall, 1990). Sciurid rodents, a large and diverse rodent family, are among the most studied food hoarders. Among tree squirrels, hoarding behaviour by red squirrels *Sciurus vulgaris* (Rice-Oxley, 1993; Jiang, 1995; Wauters and Casale, 1996; Lee, 2002; Wauters et al., 2002); grey squirrels *Sciurus carolinensis* (Thompson and Thompson, 1980; Kraus, 1983); fox squirrels *Sciurus niger* (Nixon et al., 1968; Stapanian and Smith, 1984) and Japanese squirrels *Sciurus lis* (Tamura et al., 1999) have been investigated. Food hoarding benefit animals by increasing food availability during winter and early spring (Wauters et al., 1995, 2002), and the patterns of hoarding decreases the likelihood that other foragers will find the food (Anderson and Krebs, 1978; Smith and Reichman, 1984; Stapanian and Smith, 1984; Brodin and Ekman, 1994).

MacDonald (1976) suggested that the likelihood of pilferage determines cache strategy, which is in turn affected by the age, sex, reproductive status (Clarke and Kramer, 1994) and dominance status of the food hoarder (Jenkins and Breck, 1998). Food characteristics can also affect hoarding decisions made by animals. For example, animals usually carry their preferred food items further to hoard item (Tamura et al., 1999; Lee, 2002; Vander Wall, 2003). In addition, different rodent species may play different roles in seed fate and seedling recruitment, which in turn may depend on tree species. Few experimental studies have focused on animals selecting and hoarding nuts of different tree species with different size and energy content.

David's rock squirrel *Sciurotamias davidianus* occurs widely in mountainous and hilly areas in north China, they are semi-aboreal and inhabit relative open habitats such as broad-leafed forests, conifer forests, orchards or scrub (Shou, 1962; Chen et al., 2002). In a similar way to other temperate tree squirrels, David's rock squirrels do not hibernate, and are diurnal with activity peaks in early morning and late afternoon. David's rock squirrels prefer to eat oleaginous seeds and nuts of Chinese pine *Pinus tabulaeformis*, walnuts *Juglans regia*, wild apricots *Prunus armeniaca* (Shou, 1962; Chen et al., 2002). We expect that they scatter hoard food to survive periods of food shortage in winter and early spring, and to prevent their hoarded food from being taken by other individuals of the same and different specires. Chen et al. (2002) has suggested that they store some nuts in tree holes. However, the details of food hoarding behaviour by David's rock squirrels remained unknown.

We conducted a series tests to develop an understanding of hoarding behaviour of David's rock squirrels, and to get some insight into the role of squirrels in tree regeneration under natural conditions. The study aims: 1) to describe the hoarding behavior of David's rock squirrels (larder vs scatter hoarding); 2) to test how squirrels respond to perceived pilferage of their hoarded food; and 3) to investigate difference of caching behavior of squirrels on nuts of two tree species.

1 Material and methods

1.1 Study site

The study area, Liyuanling village (40°00′N, 115°30′E) in Mentougou District, lies at an elevation of about 1 100 m and about 120 km northwestern Beijing, China. This area belongs to the Donlingshan Mountain region and has a warm temperate continental monsoon climate. The local ecosystem had been severely disturbed due to extensive wood cutting and grazing by livestock for almost a century. Since the 1990s, all villagers have been vacated from the village for restoration and conservation of local ecosystem. Liaodong oak *Qercus liaotungensis*, wild apricot *P. armeniaca*, *Vitex negundo* and *Prunus davidiana* are common shrubs. Under shrublands, *Elymus excelsus*, *Poa* spp., *Elsholtzia stauntoni* are common grass species. Larch *Larix principis-rupprechtii* and Chinese pine *P. tabulaeformis* have been planted in small areas by a local reforestation farm. Wild apricot typically set fruits from June to August, while walnuts *J. regia* are available from September to October. The area is within the natural distribution of David's rock squirrels (Shou, 1962; Chen et al., 2002).

1.2 Enclosure design

Four separate outdoor enclosures (4 m× 3 m× 1 m) were constructed using iron sheets in a flat abandoned farmland. To prevent experimental animals from escaping, the foot of iron sheets was buried 30 cm and the top of enclosure was covered with wire-meshes (2.5 cm × 2.5 cm in mesh size). All the vegetation was removed leaving the enclosure floor barren. A wooden nest box (30 cm × 20 cm × 20 cm), with a water bottle attached, was placed in one corner inside enclosure. All food items were placed in a wooden feeder (25 cm× 25 cm× 1 cm) located in the enclosure center. The central feeder location forced subjects to cross open space to get from the nest box to the food source and from the food source to potential sites for scatter hoarding. Enclosure was divided in four quadrants with the feeder as the origin in ease of mapping cache location.

1.3 Experimental animals

Twelve adult David's rock squirrels (6 males, 6 females), with mean (± *SD*) body mass of 264 ±

25 g for males, and 247 ± 28 g for females, were live captured from the study area. Their previous dietary experience was presumed to have consisted primarily of the predominate vegetation. When captured animals were weighed, examined to ensure they were healthy and to determine gender and tagged for subsequent identification. All subjects were individually maintained in cages (45 cm× 30 cm× 30 cm) specially made of wire mesh (2.5 cm× 2.5 cm in mesh size). The room where animals were housed was kept on natural photoperiod. Animals were fed *ad libitum* with' non-test food', mixed pellet fodder for rabbits, and drinking water.

1.4 Nut collection and marking

Food items offered squirrels during the study were seeds of wild apricot and walnuts. During fruiting periods (July and September), matured intact seeds of wild apricot and walnuts were collected, and kept hermetically until experimental use. We selected these two nuts because they are wildly available, and important in the diet of David's rock squirrels at the study area, and because they are relatively large and easy to experimentally manipulate. Squirrels caught in the area were presumed to have had prior experience with both these food items. Walnut is much bigger than seed of wild apricot, and their fresh mass were 10.74 ± 1.42 g ($n = 50$) and 1.19 ± 0.17 g ($n = 50$), respectively. Individual nuts were marked following Zhang and Wang (2001). Tiny hole was drilled at the spine of each seed, and small, light tin-tag (3 cm long and 1 cm wide) was connected with fine wire of 3 cm long. The tags were coded using a sharpen metal-pen. Tags were easily seen after the seeds buried by squirrels because the tags were left on the ground surface. Weight of the metal tags (0.1 g) was negligible relative to the weight of the food item. Former studies indicated that attaching these tags did not significantly influence the transport and burial of tagged seeds by rodents (Li and Zhang, 2003).

1.5 Experimental procedure

The study was carried out during September – October, 2002. A animal was randomly assigned to one of the 4 enclosures. Animals were food deprived for 6 hours prior to being placed in their respective enclosure and allowed 3 hours to adapt to their new environment. To avoid potential conflict with the daily activity peak, squirrels were put in enclosure at 13:00 on the first day (day 0). Ten marked walnuts and 20 seeds of wild apricot were then placed in each centrally located feeder. At the same time of the next day (day 1), all food items were examined and location of moved and buried food items were identified. Food items were recorded as fitting one of 5 categories as follows: EI-eaten *in situ*, the tagged seeds were eaten in the feeder; ER-eaten after removal, the tagged seeds were eaten on ground surface after removal; B-buried, the tagged seeds were buried in soil inside enclosure; EN-entered nest, the tagged seeds were transported into nest-box; AS-abandoned on the surface, the tagged seeds were abandoned on ground surface after removal.

After checking and recording, all food items were removed from enclosures, which simulate pilfering on hoarded food by other squirrels. The procedures were then repeated with new wild apricot seeds (20) and walnuts (10). Subjects were removed at the end of each trial and the nest box, feeder, and the enclosure were thoroughly cleaned. An additional 4 squirrels were then randomly assigned to the enclosure and the test was repeated. Subjects were tested only once. During the three day's experiment (day 0 – day 2), 12 subjects were tested, and a total of 20 walnuts and 40 wild apricot nuts were offered to each subject.

We defined those food items transported into nest-boxes as larder hoarding, while any food items buried in soil within enclosures as scatter hoarding (Smith and Reichman, 1984; Vander Wall, 1990; Jenkins and Breck, 1998).

1.6 Statistical analyses

SPSS for Windows (version 10.0) was employed for statistical analyses. Wilcoxon test was used to compare the difference: 1) in the number of walnuts between larder and scatter hording; 2) in the number of larder hoarded nuts of wild apricot and walnuts; 3) in the number of removed food items from feeder between day 1 and day 2; 4) of scatter-hoarded walnuts between day 1 and day 2; and 5) of transportation distance of seeds of wild apricot and walnut abandoned on surface. Paired-sample t test was used to determine the differences, between day 1 and day 2, of the transportation distances of buried food items. Chi-square test was used to determine whether the buried food items distribute randomly among four quadrants within enclosure or not; 1 sample Kolmogorov-Smirnov test was used to examine whether the distribution pattern of transportation distance of buried walnuts was normal. We did not compare the difference of the nuts eaten in nest because of their few numbers.

2 Results

2.1 Hoarding strategy

From day 0 to day 1, none of the seeds of wild apricot and walnuts was eaten in the feeder (EI). Significantly more walnuts were buried (B) (32.50%) than those transported into nest box (EN) (2.50%) (Wilcoxon test, $Z = -2.117$, $P = 0.034$). None of the nuts of wild apricot was buried though several were taken back to nest box (Table

1). Squirrels took more (2.5%) walnuts than seeds of wild apricot (0.42%) into nest box (Wilcoxon test, $Z = -4.122$, $P = 0.000$). Nonetheless, some squirrels used a larder strategy as some food items were taken into nests. Those walnuts were usually buried alone; no caches were found with more than a single walnut. Buried walnuts were not randomly distributed among quadrants (Chi-square test, $\chi^2 = 8.7864$, $df = 3$, $P = 0.032$) (Fig.1). The mean distance between the feeder and buried walnuts was 171.77 ± 39.34 cm (Table 2), and the distance walnuts were moved fit a normal distribution pattern (Kolmogorov-Smirnov test, $Z = 0.799$, $P = 0.547$).

Table 1 Fate of nuts handled by 12 David's rock squirrels on day 1

Nut types		Behaviour categories				
		Entered nest	Buried	Abandoned on surface	Eaten *in situ*	Eaten after removal
Walnut	Mean ± *SD*	0.25±0.62	3.25±3.84	1.67±2.67	0	0.01±0.29
	Range	0−2	0−10	0−9	0	0−1
	Total number of seeds	3	39	20	0	1
Wild apricot	Mean ± *SD*	0.08±0.29	0	2.25±2.18	0	0.25±0.87
	Range	0−1	0	0−6	0	0−3
	Total number of seeds	1	0	27	0	3

Table 2 Statistic of transportation distances of B and AS food items

Time	Food items	*n*	Buried		Abandoned on surface	
			Mean ± *SD* (cm)	Range (cm)	Mean ± *SD* (cm)	Range (cm)
Day 1	Walnut	12	171.77±39.34	90−235	139.95±89.44	5−245
	Wild apricot	12	0	0	49.96±65.45	4−230
Day 2	Walnut	12	154.13±48.64	27−246	148.30±85.37	5−237
	Wild apricot	12	0	0	77.26±79.05	4−230

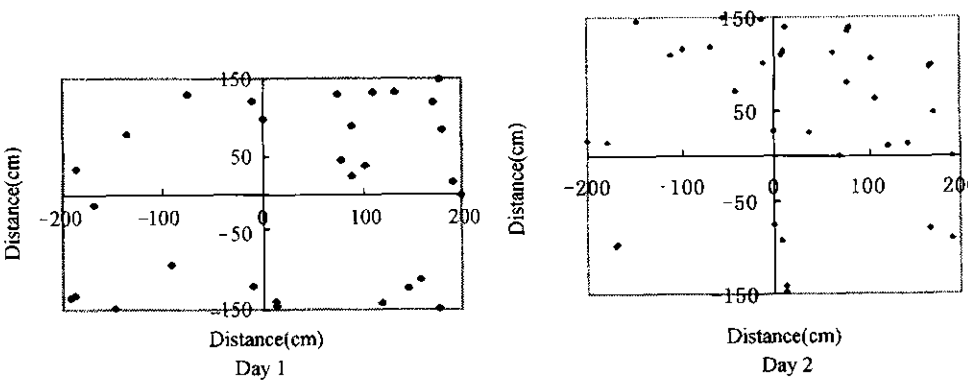

Fig.1 Distribution pattern of nuts of walnut buried by David's rock squirrels within the enclosures

Feeders was placed at center with a coordinate of (0, 0), the nest box was placed at top left corner.

2.2 Response to simulated pilferage on hoarded food

On day 2, all food items were removed, which simulated pilfering by other squirrels. The result shows that David's rock squirrels, when confronted by perceived pilferage on hoarded food, changed their hoarding strategy accordingly. They continuously scatter hoarded more walnuts (37.5%) than larder hoarded (3.33%) (Wilcoxon test, $Z = -2.371$, $P = 0.018$). Overall, squirrels removed significantly more walnuts from feeders on day 2 than that of day 1 (Wilcoxon test, $Z = -1.793$, $P = 0.049$) (Table 3), and nuts of wild apricot was transported into nest on day 2 (Table 1). However, there was no significant difference on removed seeds of wild apricot between day 1 and day 2 (Table 2). Though David's rock squirrels took more walnuts on day 2, but the difference between the two days was insignificant (Wilcoxon test, $Z = -0.527$, $P = 0.598$). Scatter-hoarded walnuts were not randomly distributed (χ^2

$=11.7975$, $df=3$, $P=0.008$) (Fig.1). Mean distance squirrels buried walnuts from the feeder on day 2 was 154.13 ± 48.64 cm (Table 3), and this distance was shorter than that of day 1 (the difference was insignificant but $t=2.001$, $df=38$, $P=0.053$), and fit a normal distribution pattern (Kolmogorov-Smirnov, $Z=0.741$, $P=0.643$). Cache size of walnuts on day 2 again was limited to a single walnut. Again none of seeds of wild apricot transported by squirrels on day 2 was buried.

Table 3 Fate of nuts handled by 12 David's rock squirrels on day 2

Nut types		Behaviour categories				
		Entered nest	Buried	Abandoned on surface	Eaten *in situ*	Eaten after removal
Walnut	Mean ± *SD*	0.33±0.65	3.75±3.96	2.75±3.02	0	0
	Range	0-2	0-9	0-5	0	0
	Total No. of nuts	4	45	33	0	0
Wild apricot	Mean ± *SD*	0	0	2.92±1.62	0	0.50±1.00
	Range	0	0	0-5	0	0-3
	Total No. of nuts	0	0	35	0	6

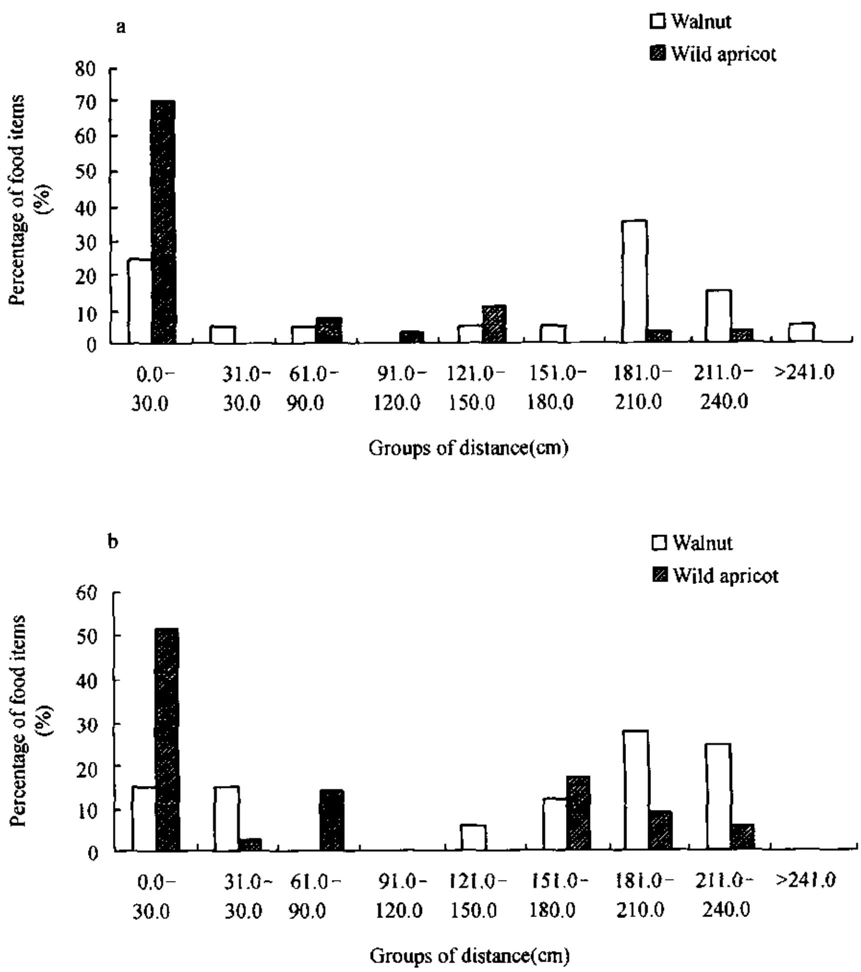

Fig.2 Percentage distribution of food items abandoned on the top of surface within enclosures
Letters a and b show the results of day 1 and day 2, respectively.

2.3 Difference of treatment between two food items

David's rock squirrels behave differently in handling walnuts and seeds of wild apricot, they larder hoarded both two nuts in nest box, and only walnuts were scatter hoarded (Table 1, Table 2). Subjects did not eat any of the two food items *in situ*, but consumed (ER) more seeds of wild apricot (1.25%) than walnuts (0.83%) on day 1 (Wilcoxon test, $Z=$

−3.011, $P = 0.003$) and day 2 ($Z = -3.697$, $P = 0.000$) (0.00% and 0.25% for walnuts and wild apricot, respectively) when taking nuts away from feeder. The mean distance between the feeder and AS seeds of wild apricot was significantly shorter than that of walnuts on both day 1 (Wilcoxon test, $Z = -2.696$, $P = 0.007$) and day 2 ($Z = -3.234$, $P = 0.001$). There were 70.37% (day 1) and 51.43% (day 2) seeds of wild apricot were abandoned on surface within 30 cm from the feeder (Fig.2), indicating squirrels took larger and the preferred food items longer distance than smaller ones.

3 Discussion

The results of our study show that David's rock squirrels (*S. davidianus*) exhibit two patterns of food hoarding, and they mainly hoarded food in scatter manner. The stored food might play an important role in the late winter and early spring with poor food supply because David's rock squirrels do not hibernate (Shou, 1962; Chen et al., 2002). The squirrels, even in a confined space, tend to hoard food items widely. The result confirmed the previous observation (Chen et al., 2002), and was accordant to the result that tree squirrels are typical scatter-hoarders (Vander Wall, 1990; Tamura et al., 1999; Lee, 2002). On the other hand, scatter hoarding is a faster means of sequestering food (Hart, 1971). David's rock squirrels store food in an manner similar to North American ground squirrels (*Spermophilus*), not like tree squirrels (*Sciurus*) (Vander Wall, 1990).

When confronted by simulated pilferage on hoarded food, David's rock squirrels changed their hoarding strategy. They took more walnuts away from feeder either for larder hoarding or scatter hoarding. Similar results were reported in other species. For example, eastern chipmunks *Tamias stiatus* typically larder hoarded their food in home burrows, but in a provisioning experiment, the females with young and the juveniles scatter hoarded (Clarke and Kramer, 1994). The pilferage on hoarded food existed widely in the field (Vander Wall, 1995). Merriam's kangaroo rat shifted from mostly scatter hoarding to mostly larder hording strategy after their caches were pilfered (Preston and Jacobs, 2001).

David's rock squirrels discriminatively treated two species of nuts different in size, they failed to scatter hoarding seeds of wild apricot though ate several of them. This suggests that, in the context of the experiment, seeds of wild apricot were not very attractive to squirrels, even if the two food items were available here, and the foraging task was easy because food items were placed at feeder. So we think that several other factors than food availability are known to influence animal's food hoarding behavior. Food quality is one such factor (Tamura et al., 1999). Compared with seed of wild apricot, walnut is larger, and therefore more nutritious and deserves to hoard by animals. In other words, in one caching bout, animal will gain more benefits from selecting walnuts. Eurasian red squirrel *S. vulgaris* also selected food items of high energy content for hoarding, in preparation for winter and the breeding season (Lee, 2002). Except for difference on nutritional composition, seeds of wild apricot and walnuts differ obviously in size. Scatter hoarding animals are more likely to eat small seeds and are more likely to hoard larger seeds (Vander Wall, 2003). Forget et al. (1998) carried out a study on the effects of (conspecific) seed size on caching behaviour of agoutis *Dasyprocta punctata* and other rodents on Barro Colorado Island, Panama and found that predation of the smallest seeds (<1 g) was usually equivalent to removal. Jansen et al. (2002) found that the probability of red acouchies *Myoprocta exilis* eating, rather than caching, *Carapa* nuts increased with decreasing seed mass.

Another factor may be the handling time of food items (Jacobs, 1992). The handling time for a walnut will be longer than that on a seed of wild apricot because of larger size and thicker seed coat. In the field, handling time is inevitably related to predation risk (Clarke and Kramer, 1994; Lima, 1998). This result might indicate that, under natural conditions, David's rock squirrels consume more wild apricot seeds in short term, while store walnut for later use.

The mean distance of moved walnuts was greater than that in seeds of wild apricot. Some other studies also showed similar results, for example, red squirrel *Tamiasciurus hudsonicus* (Hurly and Robertson, 1987), yellow pine chipmunks *Tamias amoenus* (Vander Wall, 1995), Japanese squirrel *S. lis* (Tamura et al., 1999), and Merriam's kangaroo rats *Dipodomys marriami* (Leaver and Daly, 1998) hoarded their preferred food items at a larger distance from the source. On the other hand, hoarding further away may be advantageous for squirrels because lower risk of pilfering (Vander Wall, 1990; Tamura et al., 1999). In general, David's rock squirrels will transport and hoard larger energy-rich food items in longer distance. The implication of our study is that David's rock squirrels may play a positive role in regeneration of walnut tree through scatter hoarding, while play small role in facilitating natural regeneration of wild apricot. This issue deserves in-depth research in the future.

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岩松鼠的食物贮藏行为

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