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Effects of foraging experiences and memory of food locations on cache detection by *Apodemus speciosus* mice.

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Introduction

Some animals cache surplus food for later use when they are temporarily provided with abundance [17]. This hoarding activity is prevalent among granivorous mammals, such as mice, chipmunks, and squirrels [2, 12, 13, 16, 20]. These rodents usually transport and cache seeds in the surface layer of the soil where physical conditions are favorable for cached seeds to retain the ability to germinate [17].

Cached seeds are recovered by the hoarders or pilfered by animals other than the hoarders (naïve competitors) [1, 11, 14, 16]. Mammals use a variety of cues, such as olfactory and visual cues, in the search for and detection of cached food [4, 5, 8–10, 18]. Naïve competitors rely on only olfactory and visual cues in cache detection while the hoarders may also use the memories of their own cache sites [7, 20]. Therefore, the recovery ratio of caches by cache owners is higher than the pilferage ratio [1, 16].

Apodemus mice inhabit a wide range of forests in Japan. They are known as the acorn predators and acorn dispersers of *Pasania edulis*, a dominant tree species in laurel forests in southern Kyushu [12, 13]. Sone and Kohno [13] have reported that *Apodemus* mice cache acorns in their own home ranges, that these cache sites are concentrated in certain areas and had similar topographical and geographical characteristics, as Vander Wall [20] described for chipmunks. The recovery and/or pilferage ratios of caches are affected by the density and spatial arrangement of caches; more caches are recovered or pilfered in areas where caches are concentrated [2].

Animals may use their past experiences in their food searching activities [10, 20]. Stephens and Krebs [15] stated that after animals found food by chance, they changed their searching behavior from random to directed-random and concentrated their searching efforts on the area where they had found food. If *Apodemus* mice change their food searching behavior as Stephens and Krebs [15] stated, they will concentrate their searching efforts in the surrounding areas of detected caches or try to search eagerly for sites with similar characteristics to the cache sites they have found. In these cases, it is expected that the pilferage ratio of cached items by naïve competitors would increase and the fitness of hoarding activities would decrease.

Here, we conducted a series of indoor experiments to reveal how foraging experience affected future food searching behavior. We fixed or changed food stations and recorded the food searching behavior of the mice. In addition, to study the effects of cache-searching experiences on cache detection, we conducted field experiments where we buried *P. edulis* acorns in the soil and recorded their removal by *Apodemus* mice. From the results of the experiments, we discussed how the foraging experiences affected the food searching and cache detection behavior of *Apodemus* mice. We found that *Apodemus* mice frequently recovered their own caches and re-cached them in the field [1, 13]. We also briefly discuss the adaptive values of re-caching by the hoarders.

Materials and methods

Indoor experiments

Indoor arena: We conducted experiments in a 2.8×2.8 m indoor arena at the Forestry and Forest Products Research Institute (FFPRI) at Tsukuba, Ibaraki Prefecture, from December 1990 to March 1991. We set a nest box at the center of the arena and four stations at the same distance from the nest box. At each station, a shallow dish (20×25×2 cm) was set on a tension balance (Mettler 3000PM, Germany) covered with acrylic plates. Each station had two slopes on which the mouse could approach the dish on the balance (Figure 1).

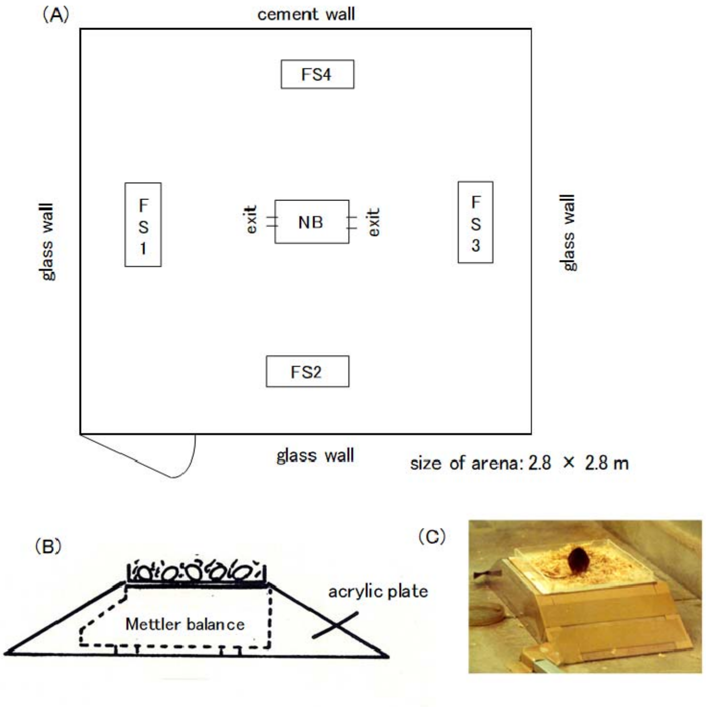


Fig. 1. Arrangement of nest box (NB) and food stations (FS1-4) in the experiment arena (A) and the features of a food station (B, C)

Mice used in the experiment: We used one male (*As* 1) and five female (*As* 2, *As* 3, *As* 4, *As* 5, *As* 6) *A. speciosus* mice. These mice had been caught in the Tochigi Prefecture in central Japan, and housed individually in a cage with artificial diets for more than six months to lessen the effects of foraging experiences in the field on the results of the experiments. The body weight of the mice used in the experiments was 22.1–36.7 g.

Experimental design: The experiment was conducted for 12 successive nights (run 1–12) for each mouse. During the first four nights (run 1–4), we placed 20–35 pumpkin seeds as food, depending on the body weight of each mouse, with 12–18 g of sawdust and 10 dummy food pieces made of hard paper on the dishes at all stations in order to examine whether each mouse had a special preference for a particular station (control session). To examine whether food searching behavior was affected by the foraging experiences of the previous night(s), we placed the food at only one station (food station) and only sawdust and dummy food at the other three stations for the next eight nights. During the 5th to 8th nights (run 5–8), the food station was fixed (fixed session). During the last four nights (run 9–12), a food station was selected randomly among the stations where we had not placed food the previous night (random session). Therefore, the food station was changed every night during the random session.

We released a mouse in the arena in the evening and recorded the time and amount of each drastic change in the load of each balance during the night. A drastic change in the load indicated that the mouse had visited or left the station. We also determined whether the mouse handled food at each respective visit to a food station based on the difference in the loads of the balance before and after the visit. The next morning, we counted the number of remaining pumpkin seeds and placed new pumpkin seeds, sawdust, and dummy food at each station in the evening. During the daytime, the mouse was kept in the nest box and not allowed to feed.

Data analysis: We compared the numbers of visits and handled pumpkin seeds at each food station in the control session using Friedman two-way analysis of variance by ranks to determine whether the mouse preferred a particular station. We examined the tendency of the mice to visit a food station intensively using a $\chi 2$-test. When we analyzed the data, we excluded the data of the visits to the stations after all food was handled.

Field experiments

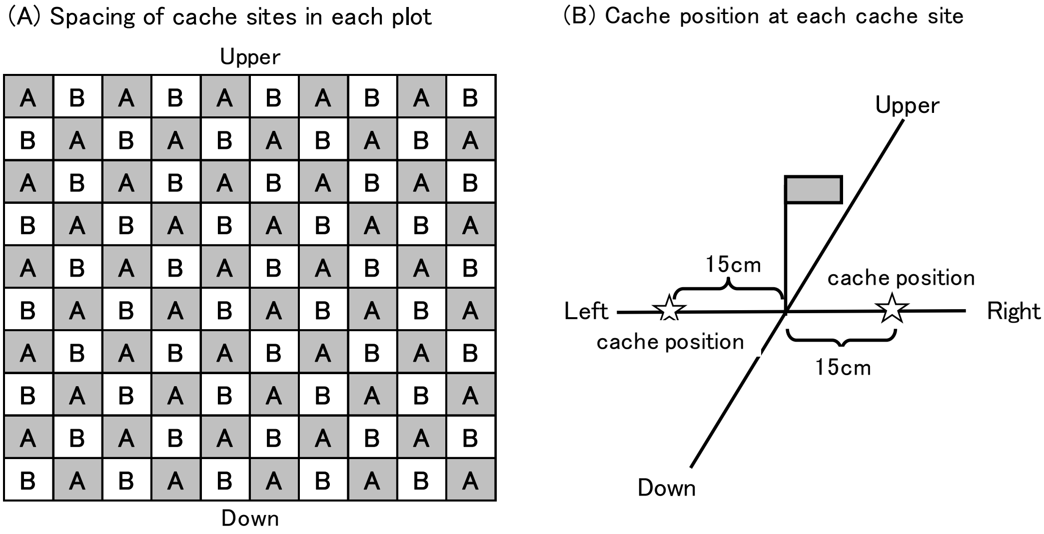
Study site: We conducted field experiments in a mature stand of *Chamaecyparis obtusa* mixed with *Quercus glauca*, *Cinnamomum camphora*, and *Auleurites cordata* at the Tama Forest Science Garden of FFPRI, Tokyo, in October and November 1992. We set up two plots about 30 m from each other, Plot 1, which had little ground vegetation, and Plot 2, which had some ground vegetation. On each plot, we set 100 (10×10) stations at 1 m intervals (Figure 2A). We marked each station with a steel stick that was 2 mm in diameter and 15 cm long and had a small piece of red vinyl tape attached (Figure 2B). During the study period, three and two *A. speciosus* mice were captured near Plot 1 and 2, respectively [12, 13].

Experimental design: The experimental design is shown in Table 1. We conducted the first, second, and third field experiments starting on October 28, November 9, and November 16, respectively. In both plots, we buried *P. edulis* acorns 1–3 cm deep in the soil at a position 15 cm to the left or right of a stick (cache position) at 50 alternate stations (cache stations) A or B, as shown in Figure 2A. The depth of the buried acorns coincided well with that of the acorns scatter-horded by *Apodemus* mice in the stand [12, 13]. In the first and the second experiments, the site of the cache stations (A or B) and cache positions (left or right) were the same in the two plots. In the third experiment, however, the cache stations were on Plot 1. We buried acorns at another 50 stations but did not change the cache position at each station. On Plot 2, we did not change the cache stations but did change the cache position from the left to the right of the stick. After burying the acorns, we checked the buried acorns every morning until all acorns had disappeared. We also recorded the digging tracks left by the mice at each station in the third experiment.

Table 1 Experimental design (hoarding site and position) of the field experiment

Experiment	Hoarding date	Plot 1		Plot 2	
		Station	Position	Station	Position
First	Oct. 28, 1992	B	right side	A	left side
Second	Nov. 9, 1992	B	right side	A	left side
Third	Nov.16, 1992	A	right side	A	right side

Station A and B are shown in Fig. 2A and Position in Fig. 2B.



(A) Spacing of cache sites in each plot

Upper

A	B	A	B	A	B	A	B	A	B
B	A	B	A	B	A	B	A	B	A
A	B	A	B	A	B	A	B	A	B
B	A	B	A	B	A	B	A	B	A
A	B	A	B	A	B	A	B	A	B
B	A	B	A	B	A	B	A	B	A
A	B	A	B	A	B	A	B	A	B
B	A	B	A	B	A	B	A	B	A
A	B	A	B	A	B	A	B	A	B
B	A	B	A	B	A	B	A	B	A

Down

(B) Cache position at each cache site

Fig. 2 Spacing of cache stations (A) and cache positions (B) in the field experiment.

Cache stations were arranged at 1 m intervals.

Results

Indoor Experiments

Table 2 shows the results of a Friedman two-way analysis of variance by rank for the number of visits to each station and that of the pumpkin seeds handled at each station in the control session. The number of visits (*As*1–*As* 6) did not significantly vary with the station except for *As* 4, who visited St. 3 and 4 more frequently than the other stations. In addition, the number of acorns handled at each station did not differ significantly according to the mouse. These results suggest that none of the mice had a special preference for particular stations in the arena.

Table 2. The results of Friedman two-way ANOVA by ranks for the number of visits to and that of punpkin seeds handled at four food stations in control session (Indoor experiment)

Mice	No. of visits to bait stations		No. of handled pumpkin seeds	
	χ^2_r-values	*P* -values	χ^2_r-values	*P* -values
As 1	1.000	0.931>*P*>0.653	1.000	0.931>*P*>0.653
As 2	1.575	0.754>*P*>0.667	1.275	0.800>*P*>0.754
As 3	6.150	0.105>*P*>0.094	4.725	0.242>*P*>0.200
As 4	7.650	0.052>*P*>0.036	0.375	0.992>*P*>0.928
As 5	4.700	0.125>*P*>0.069	3.375	0.389>*P*>0.355
As 6	5.400	*P*=0.158	5.250	0.190>*P*>0.158

In both fixed and random sessions, all mice visited a food station more frequently (44-85% of the total visits) than the other three stations (Table 3). The intensive visits to a food station were statistically significant in 22 out of 23 runs in the fixed session and in 17 out of 20 runs in the random session (Table 3).

Table 3 The number of visits to the stations in each run of the fixed and random session and the concentration of visits to the station with food

Mouse	Session	Run	Food station	No. of visits to				χ^2-values
				St.1	St.2	St.3	St.4	
As1	Fixed	1	1	23	5	7	2	10.391**
		2	1	25	1	3	1	20.559***
		3	1	18	2	0	2	12.079***
		4	1	20	2	2	0	14.182***
	Random	1	3	16	4	19	1	4.381*
		2	2	4	9	7	2	5.246*
		3	4	2	3	2	11	—
		4	1	3	3	2	2	—
As2	Fixed	1	4	2	5	5	17	6.737**
		2	4	2	1	2	21	16.227***
		3	4	3	1	2	26	20.329***
		4	4	1	2	2	29	24.985***
	Random	1	3	4	4	24	3	13.344***
		2	1	24	3	5	5	11.822***
		3	2	4	24	5	4	11.822***
		4	3	1	0	21	0	19.948***
As3	Fixed	1	2	5	27	11	35	8.472**
		2	2	22	26	12	28	6.857**
		3	2	14	30	39	19	8.243**
		4	2	23	38	37	36	0.125
	Random	1	3	14	30	46	26	5.580*
		2	2	31	34	45	18	9.725**
		3	1	51	57	39	33	1.758
		4	4	6	8	8	8	0.301
As4	Fixed	1	2	2	23	5	3	13.223***
		2	2	6	22	9	8	5.512*
		3	2	2	11	2	1	—
		4	2	5	21	2	3	11.387***
	Random	1	4	3	12	10	22	5.716**
		2	3	4	9	21	5	6.794**
		3	2	2	19	10	3	0.449
		4	4	1	1	1	0	—
As5	Fixed	1	2	7	31	5	5	15.027***
		2	2	2	35	7	1	25.089***
		3	2	0	39	1	1	34.149***
		4	2	0	36	1	1	35.611***
	Random	1	1	18	7	3	2	7.519**
		2	4	4	3	1	33	23.323***
		3	2	1	35	0	4	31.746***
		4	4	0	0	0	0	—
As6	Fixed	1	1	48	6	10	2	30.084***
		2	1	34	1	0	2	31.385***
		3	1	40	11	5	3	21.725***
		4	1	31	23	10	10	4.743*
	Random	1	4	5	8	4	55	38.035***
		2	2	2	42	2	8	30.107***
		3	3	3	7	44	8	26.244***
		4	1	35	11	6	3	16.635***

—: The number of data was so small that a statictical analysis could not be conducted

*, **, ***: significant at *P*=0.05, 0.01, and 0.001 level, respectively.

Table 4 shows the visiting sequences of each mouse to each station in each run in the fixed and random sessions. Two mice (*As* 1 and 2) visited first the food station of the previous night (previous night's food station) in most runs in these two sessions. However, the sequence of their visits to these stations was different. *As* 2 repeatedly visited and handled food at a food station after it discovered a food station in all runs. *As* 1, however, visited the other stations repeatedly after its first food handling in six out of the eight runs.

Table 4. Visiting sequences of the mouse to each station in the fixed and random session.

Mouse	Session	Run	Food station	Visiting order						
				1st	2nd	3rd	4th	5th	6th	7th
As1	Fixed	1	1	1	3	2	①	4	3	2
		2	1	①	2	1	4	①	1	①
		3	1	①	①	{4}	{1}	{1}	{1}	{1}
		4	1	3	①	①	①	2	①	①
	Random	1	3	Ⅰ	1	③	3	2	{③}	{3}
		2	2	Ⅲ	3	4	1	②	3	②
		3	4	Ⅱ	1	4	2	4	④	3
		4	1	Ⅳ	3	3	2	①	2	{1}
As2	Fixed	1	4	4	4	3	④	④	④	2
		2	4	4	④	④	④	1	2	④
		3	4	④	④	④	④	④	④	④
		4	4	④	④	④	④	④	④	④
	Random	1	3	Ⅳ	③	③	③	③	③	③
		2	1	Ⅲ	2	①	①	①	①	①
		3	2	4	②	②	②	②	②	②
		4	3	③	③	③	③	③	③	③
As3	Fixed	1	2	4	{4}	{4}	{4}	{4}	{②}	{②}
		2	2	4	②	②	②	②	②	1
		3	2	4	1	3	②	②	②	②
		4	2	3	②	②	1	4	1	②
	Random	1	3	3	3	3	2	3	4	{3}
		2	2	1	②	3	2	②	4	②
		3	1	4	2	2	1	3	3	2
		4	4	④	④	3	2	④	④	3
As4	Fixed	1	2	1	4	3	②	2	2	3
		2	2	3	②	1	2	4	3	②
		3	2	3	4	②	1	②	②	②
		4	2	1	1	3	2	1	4	②
	Random	1	4	4	4	2	④	4	2	2
		2	3	Ⅳ	3	2	③	③	③	③
		3	2	4	3	2	2	1	3	2
		4	4	Ⅱ	1	{3}	—	—	—	—
As5	Fixed	1	2	2	②	{3}	{②}	{2}	{2}	{2}
		2	2	②	②	3	3	3	3	2
		3	2	②	②	②	②	②	2	2
		4	2	4	②	2	2	2	②	{2}
	Random	1	1	4	3	2	1	1	1	2
		2	4	Ⅰ	1	2	1	2	4	4
		3	2	2	1	②	②	2	4	4
		4	4	—	—	—	—	—	—	—
As6	Fixed	1	1	3	①	①	1	3	2	①
		2	1	4	①	①	①	①	1	{1}
		3	1	2	2	1	①	1	2	{4}
		4	1	4	4	{2}	{①}	{3}	{3}	{2}
	Random	1	4	2	④	④	④	2	1	2
		2	2	2	2	1	2	4	4	4
		3	3	Ⅱ	1	2	1	3	3	3
		4	1	①	①	①	2	2	3	1

The numbers in the table are the visited station number.
Roman numerals show that the mouse first visited the station where foods were set the previous night.
Numbers in circle show that the mouse treated foods at the station.
Numerils in parentheses show that the mouse visited the station in the second or later runs.

Three mice (*As* 3, 4, and 6) did not visit the previous night's food station first in most runs, if any, in these two sessions. *As* 3 visited a food station and handled food repeatedly once it discovered a food station in the fixed session, but not in the random session. *As* 4 did not handle food at the first visit to a food station and did not handle food repeatedly after the first food handling in many runs during both sessions. *As* 6 tended to visit a food station repeatedly and handled food several times after its first visit to a food station.

The other mouse, *As* 5, visited a previous night's food station first in three out of four runs in the fixed session, but only in one run in the random session. After the first visit to a food station, the mouse repeatedly visited a food station and handled food in the fixed session. In the random session, the mouse showed the same foraging behavior as in the fixed session, but this tendency was less apparent.

Field experiments

Figure 3 shows the temporal patterns of the disappearance of the buried acorns. In Plot 2, the acorns buried disappeared rapidly—within 1–3 days. In Plot 1, the number of acorns buried on November 9 (Experiment 2) decreased rapidly, as in Plot 2, but those buried on October 28 and November 16 (Experiments 1 and 3) decreased in a stepwise fashion or gradually reached zero at the tenth and thirteenth days, respectively.

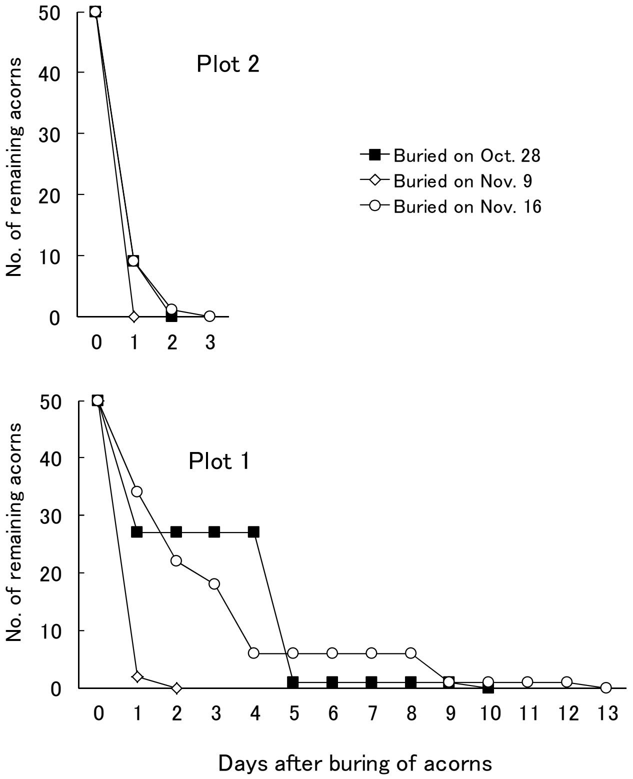


Fig. 3 Temporal changes in the number of remaining buried acorns.

In Experiment 3, mice left digging tracks in Plot 2 from November 16 to 19. During the first night (November 16/17), mice removed 41 acorns (Figure 3) and dug at three stations where an acorn had not been buried (wrong position) (Figure 4). During the second night (November 17/18), mice removed eight of the nine remaining acorns (Figure 3, Plot 2) and dug at 13 stations: 10 stations where acorns were buried (correct stations) and three wrong stations (Figure 4). At all wrong stations, mice dug at the wrong position, and at the correct stations, mice dug at the position where acorns remained or had been recovered (correct positions). During the third night (November 18/19), the last acorn disappeared (Figure 3). Mice dug at five correct stations. At four of the five stations, they dug at the correct position (Figure 4). Thus, the ratio of the number of digging tracks at the correct position to those at the wrong position was 0, 7/6 and 3 on the first, second and third nights, respectively.

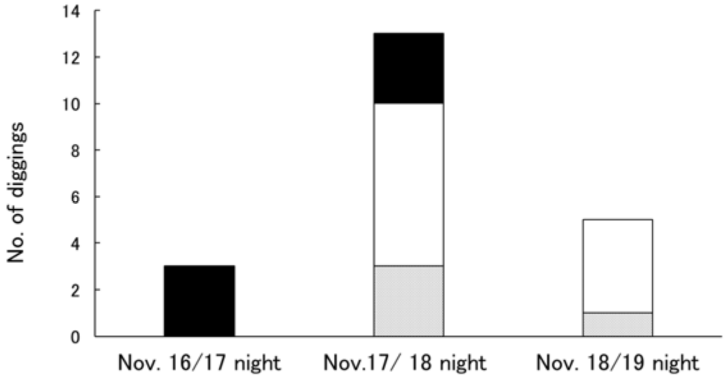


Fig. 4. The number of the digging tracks left by the mice in Plot 2 during the third experiment.

The tracks were observed at wrong positions in wrong stations (solid), correct positions in correct stations (open) and wrong positions in correct stations (dotted).

Discussion

Some animals cache surplus food for later use [17]. Cached food is usually recovered by the cache owners or pilfered by naïve competitors [1, 12, 13]. In many cases, the naïve competitors found fewer caches than the cache owners [1, 6, 16, and so on] because the memory of the cache site provides an advantage to the cache owners in recovering their own caches. However, if the naïve competitors accumulated knowledge about the cache sites of other individuals obtained through a series of cache detections and changed their searching behavior from random to directed-random [15], they would be able to detect and pilfer more caches.

Such directed-random searching was observed both in the indoor and field experiments in this study. In the indoor experiments, although the effects of food searching during the previous night varied by each mouse, three out of the six mice visited the previous night's food station first in the fixed and random sessions. More mice visited first the previous night's food station in the fixed session than in the random session. Once they had recognized a food station, they intensively visited the food station both in the fixed and random sessions. The intensive visits to a food station were more apparent in the fixed session. These results suggest that the mice may learn and memorize the spatial arrangement of food patches and these memories lead to directed-random food searching. The tendency of directed-random searching would be strengthened by repeating the same experience.

In a series of field experiments, acorns buried in Plot 2 with some ground vegetation disappeared rapidly in all experiments, but those in Plot 1, which had little vegetation, disappeared gradually or in a stepwise fashion, as shown in Figure 3. Cache searching may be influenced by ground vegetation. In the third experiment in Plot 2, mice dug at the same cache sites again after they had removed the acorns. The ratio of the number of digging tracks at the cache positions to those at the wrong position (no cache) increased from the first to third night. This suggests that the mice learned and memorized the spatial distribution pattern of buried acorns and the common characteristics of cache sites and used this information to detect buried acorns.

When we changed the cache positions in each station, the disappearance rate of acorns was similar to that of the first experiment, but when we changed cache stations, fewer acorns disappeared than in the first experiment during the first night. The memories of the spatial arrangement of cache stations were more important than those of the small-scale characteristics of the cache site (cache position in the station).

For some desert rodents and mice, olfaction may play an important role in detecting buried seeds [4, 5, 8]. The moisture condition of seeds and/or soil may be critical to the olfactory ability of the rodents to locate buried seeds [9]. When seeds are moistened, they imbibe water and release organic molecules that contribute to the emanation of relatively strong odors [3]. In the field study site, the soil was not dry, but rather moist. Therefore, it is probable that the mice used olfaction emanating from buried acorns. However, the results of the field experiments suggest that the mice rely on not only olfactory cues but also their memories of successful food searching experiences to detect buried acorns. Mc Quade *et al.* [10] also reported that gray squirrels used visual cues and space memories for localizing cached food.

Chipmunks selected cache sites that had certain common geographical or topographical characteristics [19]. Sone and Kohno [13] reported that *Apodemus* mice concentrated individual caches in some areas of their home ranges, which had similar geographical or topographical characteristics. Under these conditions, if naïve competitors find a cache by chance, they may concentrate their searching efforts in the areas where they found the cache or that have similar geographical or topographical characteristics. Daly *et al.* [2] also stated that a high pilferage ratio was recorded by concentrated caches or caches near landmarks. The changes in the food searching behavior of the mice observed in this study may increase the pilferage of cached acorns and lower the fitness of hoarding activities. In the field, mice recover and re-cache acorns repeatedly [1, 13]. This re-caching of cached items can be an adaptive tactic for hoarders to decrease the pilferage of their caches and to maintain the fitness of their hoarding activities.

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The effects of foraging experiences and memory of food locations on cache detection by *Apodemus speciosus* mice.

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Summary

We conducted indoor experiments to study how past experiences affect the food searching activities of *Apodemus speciosus* mice. The mice visited a food station more intensively when their site was fixed than they did when it changed every night. In the latter case, the mice first visited the station where food had been present the previous night. In addition, we conducted a series of three field experiments beginning on Oct. 28, Nov. 9 and Nov. 16, in Plot 1, which had little ground vegetation, and Plot 2, which had some ground vegetation. We buried cached *Pasania edulis* acorns at the same stations in the first and second experiments, but changed the site of the stations in the third experiment. The acorns in Plot 2 disappeared rapidly in all experiments, but in Plot 1, the number of buried acorns in the first and third experiments decreased gradually or in a stepwise fashion, suggesting that cache searching may be influenced by the amount of ground vegetation. Mice left tracks when they dug in the field, and the ratio of digging tracks at cache sites to that of no-cache sites increased day by day. The results of the present experiments suggest that the mice accumulated memories about the spatial arrangement and characteristics of cache sites during food (cache) searching and used them to detect other caches.

Key words: *Apodemus speciosus*, cache detection, foraging experience, memories

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