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Global and local spatial landmarks: their role during foraging by Columbian ground squirrels (*Spermophilus columbianus*)

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Abstract Locating food and refuge is essential for an animal's survival. However, little is known how mammals navigate under natural conditions and cope with given environmental constraints. In a series of six experiments, I investigated landmark-based navigation in free-ranging Columbian ground squirrels (*Spermophilus columbianus*). Squirrels were trained individually to find a baited platform within an array of nine identical platforms and artificial landmarks set up on their territories. After animals learned the location of the food platform in the array, the position of the latter with respect to local artificial, local natural, and global landmarks was manipulated, and the animal's ability to find the food platform was tested. When only positions of local artificial landmarks were changed, squirrels located food with high accuracy. When the location of the array relative to global landmarks was altered, food-finding accuracy decreased but remained significant. In the absence of known global landmarks, the presence of a familiar route and natural local landmarks resulted in significant but not highly accurate performance. Squirrels likely relied on multiple types of cues when orienting towards a food platform. Local landmarks were used only as a secondary mechanism of navigation, and were not attended to when a familiar route and known global landmarks were present. This study provided insights into landmark use by a wild mammal in a natural situation, and it demonstrated that an array of platforms can be employed to investigate landmark-based navigation under such conditions.

Keywords Landmark-based navigation · Spatial memory · Columbian ground squirrels · *Spermophilus columbianus* · Landmarks

Introduction

Animal navigation in wild environments is a crucial part of ecology. Many aspects of life such as finding refuges, food, or mates depend on the animal's ability to accurately move from one place to another. Moreover, each type of habitat has its own advantages and constraints, making certain mechanisms of navigation more favorable than others. As a result, knowing how animals orient can help to explain their behavioral interactions with their environments.

When navigating, animals usually employ multiple mechanisms which can be used simultaneously or in parallel to reach a goal (Bingman 1998; Menzel et al. 2000; Shettleworth 1998; Wallraff 2001). Landmark-based navigation, where some features of the environment serve as reference points, is one of the strategies used by many species. Based on their proximity to the destination, landmarks can be classified into two broad categories: local landmarks (positional), which are close to the goal; and global landmarks (directional), which serve as more distant cues and can be used over large spatial distances (Jacobs and Schenk 2003; Leonard and McNaughton 1990). Local cues (e.g., shrubs or logs) allow precise encoding of a location (Cheng and Spetch 1998), but they may not be as reliable as global ones (e.g., forest outlines or mountains), which tend to incorporate more invariant and unique features of the environment. To orient using global landmarks alone, however, may be more challenging, because the bearing and the distance to a goal do not change much as an animal travels through the environment (Cheng and Spetch 1998). According to the Parallel Map Theory, recently introduced by Jacobs and Schenk (2003), animals may rely on both local and global landmarks to generate two different maps—sketch and bearing, respectively—which can then be combined into an integrated map that allows animals to navigate successfully in space and perform novel shortcuts.

Multiple studies suggest that animals can remember a goal with respect to different types of landmarks. However, the relative importance of the available landmarks varies and often depends on the experimental conditions. When

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both local and global landmarks can reliably identify the location of a goal, many animals preferentially attend to more global features. For example, black-capped chickadees encode all possible cues about a rewarding feeder—its absolute position in space, local appearance, and location within the array of the other feeders. Chickadees use this information in a hierarchical manner, where the feeder's global position has prevalence over other cues (Brodbeck 1994). Extensive laboratory studies on rats also have demonstrated reliance on the extra-maze features of the testing room over intra-maze landmarks (Leonard and McNaughton 1990; Suzuki et al. 1980). Similarly, field studies on fox squirrels indicate that animals disregard cues provided by the maze itself and orient based on the information provided by the extra-maze cues (Jacobs and Shiflett 1999).

Most studies of landmark-based mechanisms of navigation have been conducted on captive animals where subjects are limited to the set of landmarks provided by the experimenter. Conducting experiments in the laboratory environment allows for the precise manipulation of cues and controls, but it is possible that spatial cues are used differently under artificial conditions compared to natural settings. In addition, in the majority of the laboratory studies “global” cues are only few meters away from the subject due to the limits of the testing room, so the scale of landmarks that can be used for precise encoding of a goal still remains unknown for many species. Therefore, more field experiments are necessary to complement the laboratory findings. While performing experiments under natural conditions is challenging, several studies have shown that laboratory techniques such as the use of maze can be successfully used on the field (e.g., Henderson et al. 2001; Jacobs and Shiflett 1999).

The goal of this study was to examine landmark-based orientation in free-ranging Columbian ground squirrels (*Spermophilus columbianus*) during foraging. These ground squirrels need to remember good foraging locations relative to their home and escape burrows. The distribution of grasses and forbs that squirrels eat is not uniform within their territories. For example, urination by ungulates creates nutrient rich patches (Day and Detling 1990), and some preferred plants such as dandelions that grow only in certain microhabitats. Thus, it is to an animal's advantage to remember the location of rich patches and to be able to return to such patches quickly after being interrupted by a predator attack or aggression from conspecifics.

Under natural conditions, Columbian ground squirrels—a highly visual species—are faced with an enormous number of visual cues that could potentially be used for orientation. Based on previous research on other rodent species, it seems likely that the squirrels attend preferentially to global, rather than local landmarks. In contrast to the cues provided to captive animals, however, the global and local landmarks available to Columbian ground squirrels are widely separated in space, and many local landmarks are often entirely unavailable. This is because the squirrels inhabit relatively flat meadow terrains where tall summer grass may prevent them (less than 30 cm tall when sitting

up right) from seeing any local features which are more than a few meters away. The edges of the meadow (forest and gorge outlines), on the other hand, can be seen from any location on the meadow and potentially represent reliable global landmarks. These global landmarks, however, are typically at a great distance from the squirrels' territories. As a result, precise encoding of a goal based only on global landmarks may be challenging.

To investigate the methods of navigation used by ground squirrels when foraging, I trained animals individually to find food that was located on a platform in an array composed of other, unbaited, platforms and a variety of landmarks. Some of the experimentally placed landmarks (flags) were always available to the animals, while others (ball, log) were present on each squirrel's territory only when experiments were being conducted. After each squirrel had learned the location of the food platform in the array, I manipulated the position of this platform with respect to experimentally introduced landmarks (flags, ball, log), naturally occurring local landmarks (vegetation pattern, burrows, rocks, bushes) and global landmarks (forest edge, the outline of the mountains), and examined the animal's ability to find the food platform.

In addition to using local and/or global landmarks for locating the food platform, animals could also potentially rely on a familiar route, either by attending to olfactory cues that had been deposited on the trail or by remembering the motor routine of getting to the food (a process also known as response learning) (Shettleworth 1998; Tolman 1948). To test the importance of a familiar route, I also examined squirrels' performances when a route was either available or absent.

General methods

Study site

Research was conducted on a 2 ha subalpine meadow surrounded by pine and spruce forest and a gorge along the Sheep River drainage (50°39'N, 114°38'W; elevation 1500 m; Alberta, Canada). During the time that experiments were conducted (June–July 2002) the grass on the meadow was relatively short (10–15 cm high) due to the cattle grazing, and animals could see above the grass when sitting upright. The population contained 54 adult females and 16 adult males. All individuals were tagged on both ears with individually numbered tags (Monel #1, National Band and Tag Company) for permanent identification. In addition, unique black marks were applied on the fur of each individual with hair dye (Lady Clairol hydrience black opal) for easy identification from a distance.

Animals

Twenty free-ranging adult female squirrels whose territories were spatially separated were chosen as subjects.

Fourteen completed the training and testing. The other six either were not interested in climbing platforms or disappeared from the meadow before training was completed. Experiments were conducted during the gestation and lactation period when females are territorial (Festa-Bianchet and Boag 1982; Murie and Harris 1988) and are highly motivated to work for a food reward. Individual territories were determined based on behavioral observations, and the positions of females and their social interactions throughout the day were recorded. Experiments with each female were done at a location that was successfully defended by her and within her territory. Territoriality prevented interference by other animals during training and tests in most cases. Animals were habituated to humans. When squirrels were approached, they hid in their burrows but quickly resumed their activities after the observer moved away a few meters.

Apparatus

A linear array of nine identical, equally spaced (0.28 m) platforms was assembled on each subject's territory (Fig. 1). As a result, each animal had a unique set of global and natural local landmarks surrounding the array. Each platform in the array consisted of a metal frame in a pyramid form (base: 0.21 m \times 0.51 m, height: 0.46 m) and a plastic cup mounted on the top to hold food. A rope was woven through one side of the frame of each platform to create a ladder for squirrels to climb. The entire platform was painted green. Only the 4th platform (#4) was baited with highly preferred food, horse feed, consisting primarily of oats. To control olfactory cues, all platforms contained oat shells that provided odor without a food reward. Moreover, prior to the experiments, the plastic cups were soaked overnight with horse feed in hot water. Squirrels could not see the food from the ground and had to climb the platforms in order to obtain it. Two local artificial landmarks, a log (0.1 m in diameter, 0.5 m long) and a ball (radius 0.06 m) on a stick (0.5 m high), were placed within the array after

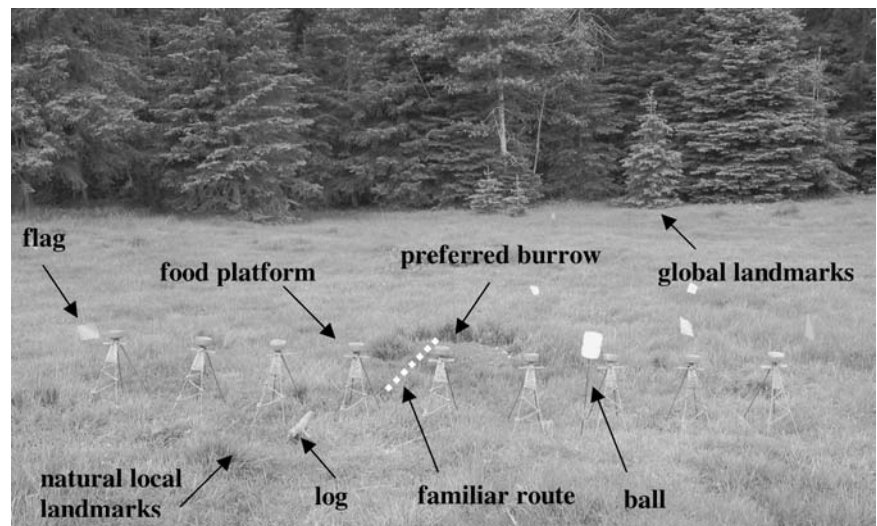
platforms #3 and #6, respectively. The small log did not hinder squirrels' approach to the platforms. Animals readily jumped over or ran on top of it if they chose to approach the platform #4 from the log side. Since the log, the ball, and the platforms were placed in each subject's territory only during experiments, they were considered to be temporary. The edges of the array were marked with orange flags (0.5 m high) that remained on the squirrel's territory even when the platforms were removed; these were considered to be local artificial/permanent landmarks. Below, the term "array" refers to the arrangement of the nine platforms, the log, the ball, and the flags.

The log, the ball, and the flags were considered to be "artificial" landmarks because they were introduced by the experimenter. However, it should be noted that "natural" landmarks such as logs also occurred in some subjects' territories. In addition, flags of different colors (non-orange) were used to mark intersection points (10 m intervals) of the grid that was laid out on the meadow, and they were constantly present on the field over a period of 10 years. Territories of all participating females contained a few flags. Natural landmarks were classified into two broad categories, local and global. Local landmarks were defined as features of the environment that were close to the array (within 10 m radius), such as rocks, small bushes or local topographical relief. Landmarks of a larger scale, like the outline of the mountains or the forest edge, were considered to be global landmarks.

Training

Each squirrel was presented with a single platform that contained food. Peanut butter was spread on the rope ladder to encourage the squirrel to climb up. After the animal learned how to obtain the reward, the whole array was introduced. During each training session, the array was placed in the same location marked by the flags to preserve the geometric relationships with the natural local and global landmarks (Fig. 1). A training session consisted of six trials. On each

Fig. 1 Training setup. The array presented to the squirrels during training, where the log, the ball are Local Artificial/Temporary Landmarks; the flags are Local Artificial/Permanent Landmarks; the vegetation pattern is one of the Natural Local Landmarks; the forest outline is one of the Global Landmarks available to the animals



trial, the squirrel was allowed to investigate the platforms. After the food was discovered the squirrel was allowed to eat a few grains; then it was chased away to a burrow. Meanwhile, the platforms occupying each position were switched around, so squirrels could not associate some features of a particular platform (e.g., olfactory or visual) with a specific position within the array. An experimenter simulated the placement of food on every platform in the array and then moved away. The actual bait was placed only on the platform occupying the fourth position in the array; the rest of the platforms contained only oat shells. The subject was then allowed to make another choice. A training session was stopped after the animal had gone to the food platform six times out of six trials or when it lost interest in the platforms and started foraging elsewhere on the meadow. An animal was considered to be fully trained if she went directly to platform #4 (the baited platform) on the first trial and continued to choose this platform in the next five trials. The number of training sessions each squirrel received varied among individuals based on their performance. On average, squirrels received $11 \pm \text{SE } 0.55$ sessions within $21 \pm \text{SE } 0.95$ days. By the end of training each squirrel had a preferred burrow to which she returned between the trials. The distance between this preferred burrow and platform #4 varied among territories ($3.79 \pm \text{SE } 0.55$ m).

After the squirrels learned to locate food consistently on platform #4, the relative position of the food platform with respect to artificial/temporary local (platform arrangement, log and ball), artificial/permanent local (flags), natural local (bushes, rocks, local topographical relief), natural global (forest edge, mountains) landmarks was manipulated in the tests described below. Tests were conducted throughout the day. Squirrels were tested individually, and the order of tests for each animal was picked at random by rolling a die.

Squirrels received retraining between each test, and were allowed to proceed to the next test only after they successfully chose platform #4 six times out of the first six trials. Most retraining consisted of only one session, and only 19% of 70 retrainings involved two sessions.

Data analysis

For each trial, I recorded the platform that the subject climbed first. The probability of a squirrel picking the “correct” platform in the array of nine platforms by chance was considered to be 1/9. I tested squirrels’ choice of a particular platform (a correct one with respect to the landmarks of interest) in each experiment against this null expectation using Binomial test. The performances among different experiments were analyzed using McNemar tests. Mann–Whitney tests were used to check whether the distance to the array from the preferred burrow had an affect on the performance.

Experiments 1–4 investigated the use of artificial landmarks in navigation by ground squirrels, while experiments 5 and 6 examined the importance of natural landmarks.

Experiment 1: local artificial/temporary landmarks shift

This experiment was designed to test whether squirrels used artificially placed local landmarks, such as the log and the ball, to locate food. These landmarks were considered to be temporary because they were present on the field only during the experiments, but were absent otherwise. The log and the ball were prominent objects in the array, close to the goal, and reliably indicated the food position during training. In the test, both the log and the ball were shifted one platform down. After this manipulation, information provided by local artificial/temporary landmarks was in conflict with cues provided by the rest of the array, the familiar route, and all natural landmarks (local and global). If squirrels relied preferentially on these local artificial/temporary landmarks, they should have searched for food on the adjacent platform downward from where food was located during training.

Method

To modify the array, the log and the ball were shifted one platform down (0.49 m). In their original location, the log was placed after platform #3 and the ball after platform #6. In the new arrangement after the shift, the log was located after platform #4, and the ball after platform #7. Food was present on platforms #4 and #5. The platform that the subject climbed first was recorded.

Results and discussion

In this test no squirrel went to platform #5, which would be the “correct” platform if the subjects had attended only to the relative locations of the log and the ball. Thirteen out of fourteen squirrels (92%) went to platform #4, the “correct” platform during training trials (one-tailed Binomial test, $n=14$, $p<0.001$).

Animals may have ignored the shift in the local artificial/temporary landmarks because they did not encode food locations using landmarks of such scale and proximity. Alternatively, because the log and the ball were on the field only during experiments, the squirrels may not have regarded them as reliable. Studies of gerbils (Collett et al. 1986) and rats (Biegler and Morris 1996) have shown that animals prefer to use landmarks that do not change their position. On the other hand, the log and the ball were present only when the array of platforms was present and could, therefore, have been more informative about food location than more permanent landmarks. To test whether ground squirrels encoded food location with respect to the other local but more permanent landmarks, Experiment 2 was conducted.

Experiment 2: local/artificial permanent landmark shift

When navigating in their environment squirrels might preferentially use local cues that are always available for

orientation. To investigate this question, the position of local artificial/permanent landmarks (flags) was shifted with respect to the food platform. The information provided by the location of the flags was in conflict with other array cues, familiar route, and all natural landmarks. If squirrels attended to the flags, they should have searched for the food in the new, shifted, location. The flags were always present on the field and potentially represented more stable and reliable reference points than did the log and the ball.

Method

The platforms, the log, and the ball were set up in their original positions, but the flags were shifted two platforms down (0.98 m). During training, the flags had been located at the beginning and the end of the array. In the new arrangement, the left flag was located between platforms #2 and #3, while the right flag was located some distance (equal to two platforms' length and a space between them) away from platform #9. Food was present on platforms #4 and #6. After completion of the test, the flags were returned to their original positions.

Results and discussion

Animals completely ignored the shift in local artificial/permanent landmarks.

Thirteen out of fourteen squirrels (92%) went to platform #4, the original food position (one-tailed Binomial test, $n=14$, $p<0.001$). No animals went to platform #6, the correct choice if squirrels attended only to the flags. In spite of the fact that flags were always visible to the squirrels, both during and between the experiments, subjects appeared not to use them as reference points. In experiment 1 the log and the ball had been shifted only 0.49 m, whereas in the second experiment the flags had been moved a distance of 0.98 m, but this increase in the conflict information provided by artificial landmarks and other cues did not have an effect on subjects' performance. Evidently, the squirrels ignored both temporary and permanent artificial local landmarks when locating the correct food platform.

Experiment 3: two platforms left-hand shift

In addition to the artificial landmarks, the platforms themselves might have served as cues for food location. It seems possible, for example, that the squirrels might have counted the platforms. Alternatively, they might have remembered that the correct platform was slightly to the left of the center of the array. To investigate these possibilities, the entire array was shifted with respect to natural local and global landmarks two platforms to the left, towards the beginning of the array. This put the information associated with the array in conflict with all natural landmarks, but all intra-array cues were in the agreement. If squirrels remembered

the relative location of the correct platform within the array, they should have continued to go to the fourth platform.

Method

The array was shifted the distance of two platforms (0.98 m) to the left so that platform #6 was in the place where platform #4 had been during training with respect to natural landmarks. The spatial arrangement between all artificial landmarks, including platforms, remained the same. However, the location of the array with respect to natural landmarks was different. Food was present on platforms #4 and #6.

Results and discussion

Thirteen out of fourteen squirrels (92%) climbed platform #6, rather than platform #4 (one-tailed Binomial test, $n=14$, $p<0.001$). No animals went to platform #4, which would have been the correct choice if they remembered or counted the platform's relative location within the array. This suggests that squirrels attended preferentially to some combination of natural local and/or global landmarks or a familiar route when locating the correct food platform.

Experiment 4: two platforms right-hand shift

Experiment 4 was analogous to Experiment 3, but in this case the array was shifted the distance of two platforms to the right, towards the end of the array. If squirrels remembered the relative position of the baited platform with respect to the other platforms in the array, they should have continued to choose the fourth platform. However, if the animals had memorized the absolute position of the baited platform on the field during the training, they should have visited platform #2.

Method

The array was shifted the distance of two platforms to the right (0.98 m), such that platform #2 was in the place of platform #4 during the original training. As in experiment 3, the spatial arrangement among all artificial landmarks within the array remained the same, but each platform had different natural landmarks compared to training. Food was present on platforms #2 and #4.

Results and discussion

Twelve out of fourteen squirrels (86%) went to platform #2 (one-tailed, Binomial test, $n=14$, $p<0.001$). No animal went to platform #4. Again, as in experiment 3, the majority of squirrels went to the platform where food had been during training with respect to natural local

and global landmarks. After the right-hand shift, the food platform that had been in the middle now appeared to be in the beginning of the array. However, this obvious change in the position of the food platform in the array did not seem to affect the direction of animals' search.

Experiments with bees (Chittka and Geiger 1995) and rats (Suzuki and Kobayashi 2000) have demonstrated that animals may be able to determine the location of food based on the number of landmarks they pass on the way to the feeder. By contrast, squirrels did not appear to count platforms when locating the baited one. Thus, although the squirrels might have been capable of using a 'counting' strategy if trained to do so, they did not independently resort to such a strategy.

Taken together, experiments 1–4 suggest that squirrels appear to ignore all types of local artificial landmarks. They appear either to memorize the food location with respect to natural local and/or global landmarks, or to remember the route to the food platform, perhaps by using olfactory cues or motor routines. Experiments 5 and 6 were designed to investigate the importance of natural local landmarks (local topographical relief, bushes, rocks), global landmarks (forest edge, mountains) and a familiar route during navigation to the food platform.

Experiment 5: 90° Turn

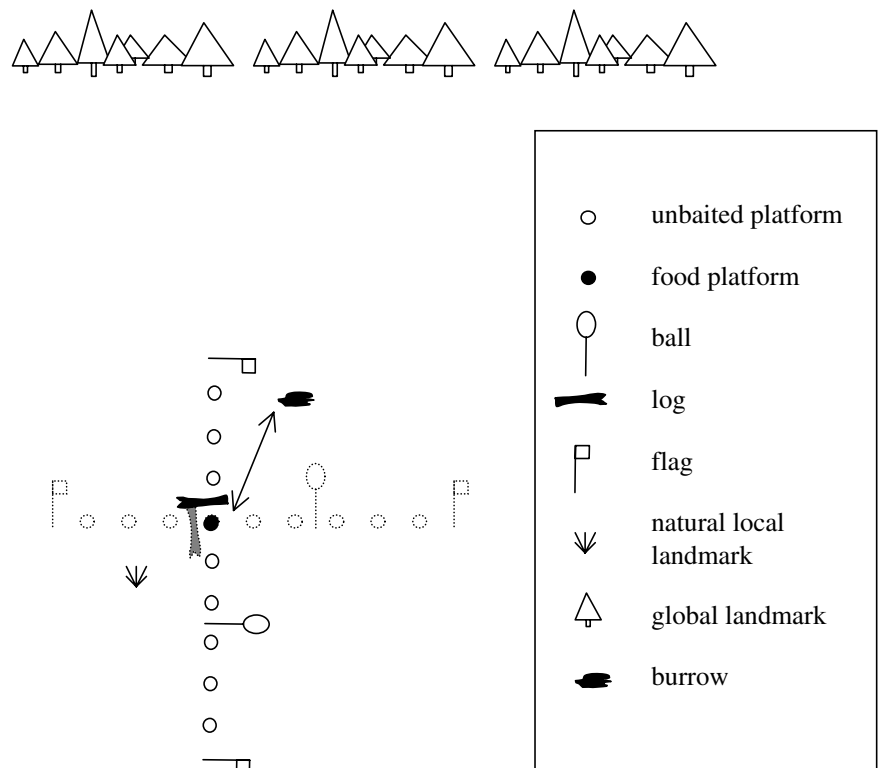
To examine the importance of global landmarks for orientation, I altered each squirrel's view of global landmarks relative the location of the array by rotating the array 90°

clockwise around the food platform (Fig. 2). When a squirrel emerged from her escape burrow, therefore, she now had to turn 90° at the burrow entrance in order to view the array. As a result, while the global landmarks of the array as a whole were altered, the food platform itself retained the familiar global landmarks. The natural local landmarks around the food platform and the familiar route from the burrow to the food platform were also unaltered. Finally, the relation among the platforms and artificial landmarks was also retained. If squirrels depended on intra-array cues, natural local landmarks, or a familiar route, their ability to find the food platform should not have been affected by the rotation. On the other hand, the degree to which natural global landmarks provided a valid reference depended on whether the food platform was encoded as a part of the array or as a separate unit. If squirrels relied on global landmarks and viewed the food platform as a part of the array, the animals' performance was expected to drop on this test.

Method

By the end of the training period each animal had a preferred escape burrow, where she hid while platforms were manipulated. The array was rotated 90° around the food platform in such a way that platform #4 stayed in its original position (Fig. 2). As a result, all natural local landmarks around platform #4 remained the same as during training, and the animal could have approached the baited platform using the same route as before. In order to see the whole array, however, the squirrel had to turn when she emerged

Fig. 2 Experiment 5: 90° Turn. The array was rotated 90° around platform #4 such that platform #4 remained in the same position as during training. Food was present on platform #4. Array's location during training is shown with dotted lines. Since the tests were conducted on the individual territories, the position of the preferred burrow with respect to the array was unique for each squirrel. The diagram represents the most typical arrangement



from the burrow and view different global landmarks than before. Food was present on platform #4.

The preferred escape burrow for one animal was in line with the array, thus the rotation did not force the animal to view new global landmarks. However, the array appeared very different with regard to the familiar global landmarks.

Results and discussion

Six out of fourteen squirrels (43%) located platform #4, a performance that was significantly better than random (one-tailed Binomial test, $n=14$, $p<0.01$) (Fig. 3). This suggests that several animals were able to derive some information from the local cues around the food platform, used familiar route or viewed platform as a unit and used familiar global cues. However, fewer squirrels went to the correct platform than had been observed in the Local Artificial/Temporary Landmark Shift experiment (two-tailed McNemar test, $n=14$, $p=0.039$). The modified view of global landmarks behind the whole array appeared to confuse about half of the animals. The distance between the preferred burrow and the food platform had no effect on the performance (Mann–Whitney test, $n=14$, $U=14.5$, $p>0.216$).

To resolve further the importance of global landmarks, a familiar route, and the type of local landmarks (natural or artificial) used by animals Experiment 6 was performed.

Experiment 6: parallel shift

In the 90° Turn experiment, animals were faced with altered global landmarks for the whole array, but the familiar route and natural local landmarks remained unchanged. The non-random choice of platform #4 on that test could have been due to squirrels using the familiar route, natural local landmarks, artificial local landmarks, or global landmarks for the 4th platform. To investigate these possibilities, squirrels were made to locate the food platform in the absence of a familiar route, natural local landmarks, and global landmarks. In this experiment, the array was shifted to the other

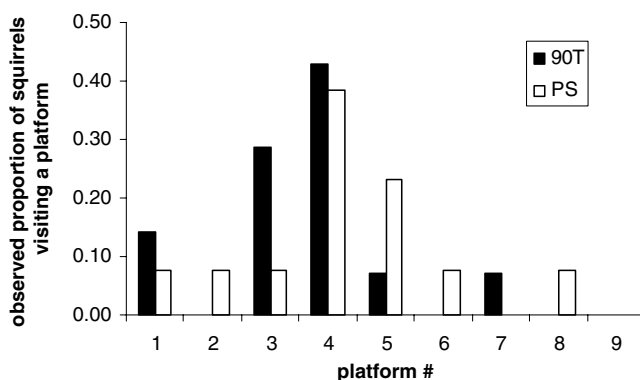


Fig. 3 Platform visits distribution on the 90° Turn (90T) ($n=14$) and the Parallel Shift (PS) ($n=13$) experiments

side of each squirrel's burrow. The position of the food platform in the array was preserved with respect to all artificial local landmarks. If a familiar route and natural local landmarks were important for navigation to the food platform, the squirrels' performance was expected to decrease on this Parallel Shift test compared to the 90° Turn test. In contrast, if global landmarks for the whole array played a prominent role in navigation, performance on the Parallel Shift and the 90° Turn tests should have been similar. If, however, squirrels encoded only the food platform with respect to global landmarks, the performance on the Parallel Shift test should decrease compared to the 90° Turn test.

Method

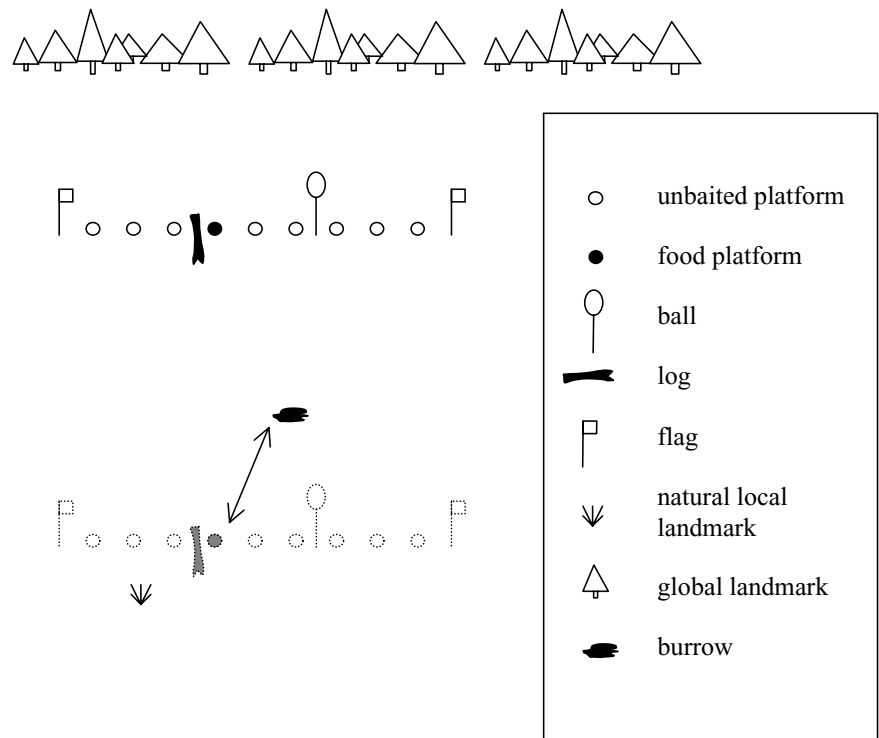
In this test, the array was shifted a distance of 4.13 m (the length of the array) from the original position to the other side of the escape burrow. Such distance insured that array was on the other side of the burrow, but still remained within the animal's territory. The distance between the new array position and escape burrow varied from territory to territory. The shift was parallel to the long axis of the array (Fig. 4). In order to see the array squirrels had to turn 180° and view different global landmarks. For one animal, the escape burrow was in line with the array during the training, so she had to turn only 50° to view the shifted array.

One squirrel had to be eliminated from the analysis because her performance on the test was interrupted by the appearance of a predator.

Results and discussion

Five out of thirteen squirrels (38%) went to platform #4 (one-tailed Binomial test, $n=13$, $p<0.01$) (Fig. 3). The distance between the preferred burrow and the food platform had no effect on the performance (Mann–Whitney test, $n=13$, $U=11.5$, $p>0.209$). This non-random choice of platform #4 suggests that some squirrels were able to use information from the local artificial landmarks when all other cues were unavailable. However, the squirrels' ability to locate the food platform on this test was significantly lower than during the Local Artificial/Temporary Landmark Shift experiment (two-tailed McNemar test, $n=13$, $p=0.039$). These results imply that having only familiar artificial local landmarks is not sufficient for many animals. In addition, the number of animals to choose platform #4 on the 90° Turn and the Parallel Shift tests was similar (two-tailed McNemar test, $n=13$, $p=1.0$). It was hard to tell whether certain individual squirrels performed consistently better than others due to a small sample of individual squirrels. Three animals made a correct choice and six an incorrect choice in both experiments, while four squirrels performed differently in two experiments. The comparison between the 90° Turn and the Parallel shift experiments suggests that the presence of a familiar route and natural local landmarks appeared to be insufficient for many animals to locate the baited platform. Moreover, the presence

Fig. 4 Experiment 6: Parallel Shift. The array was shifted a distance of 4.13 m parallel to its long axis to the other side of the preferred burrow. Food was present on platform #4. The array's location during training is shown with dotted lines. Since the tests were conducted on the individual territories, the position of the preferred burrow with respect to the array was unique for each squirrel. The diagram represents the most typical arrangement



of familiar global landmarks just around the food platform in the 90° Turn test did not improve their performance.

The fact that squirrels went to the array in both tests suggests that the array on its own served as an important landmark. Ten animals went directly to the array, but three squirrels first ran towards the training location of the array. The behavior of these three animals is similar to what was observed by Devenport and Devenport (1994). In their experiments chipmunks and golden-mantled ground squirrels did not use the appearance of the feeder to locate its position. When the feeder was moved the animals first visited the original location rather than the clearly visible feeder. In the present experiments the array was set up on the field only during training and testing, while the feeder was constantly present at the site in Devenport and Devenport's study. Perhaps, this explains that the majority of Columbian ground squirrels first looked for the array.

Interestingly, in the 90° Turn and the Parallel Shift experiments some squirrels that did not make the correct choice (90° Turn: four out of eight; Parallel Shift: three out of eight squirrels) tended to go to the platforms adjacent to the 4th platform (Fig. 3), implying that they paid some attention to the spatial arrangement of the platforms within the array.

Comparisons among experiments suggest that the alteration of global landmarks significantly affected performance. Thus, when familiar global landmarks and route were present animals did not seem to use the information provided by the spatial arrangement of the array (experiments 1–4). In the absence of known global landmarks, however, animals attended more to the relative position of the food platform within the array (experiments 5 and 6). It

appears that the use of spatial intra-array cues depends on how strongly other cues are manipulated.

General discussion

The goal of this study was to investigate landmark-based navigation by a mammal under natural conditions and provide information for comparisons with laboratory findings. The study demonstrated that an array of artificial feeders can be used to test the importance of different landmarks for orientation by wild rodents. A series of six experiments revealed that squirrels disregarded information provided by artificial local landmarks when a familiar route, natural local, and global landmarks were available to them. However, when known global landmarks were not present, animals seemed to be able to refer to the spatial arrangement of the array. For many individual squirrels, having a familiar route and natural local landmarks in the absence of known global landmarks was not sufficient for precise navigation. Thus, although squirrels might have relied at least in part on known trails when locating food, additional information from the environment was necessary for highly accurate navigation.

Several studies previously reported that some animals tended to remember a goal with respect to landmarks near it, while others ignored this type of information. For example, European jays paid more attention to near landmarks compared to more distant objects when looking for peanuts (Bennett 1993). The direction of search in pigeons was also more affected by manipulation of landmarks closer to the goal (Cheng 1989). On the other hand, Clark's nutcrackers ignored objects or ground markings near their cache sites

(Balda et al. 1986). Mice also disregarded information provided by landmarks placed inside the testing arena when looking for the nest entrance (Alyan and Jander 1994). Therefore, the finding in experiments 1 and 2 that squirrels ignored very ‘obvious’ local landmarks such as flags, the ball, and the log is not surprising and seems to be similar to behavior observed for some other animals.

Experiments 3 and 4 revealed that squirrels did not use the spatial arrangement of the platforms when a familiar route and global landmarks were present. These findings are consistent with the results obtained in the laboratory studies on cats and dogs. There, the animals did not memorize the position of the correct screen relative to the other screens when searching for an object hidden behind one of screens in an array (Fiset and Dore 1996; Fiset et al. 2000). Similar results were obtained in maze experiments with free ranging fox squirrels, which appear to ignore local cues such as the color of the maze ladders or their relative position with respect to each other, and base their search for the reward on extra-maze landmarks (Jacobs and Shiflett 1999). Interestingly, hummingbirds in analogous field experiments demonstrated the use of both extra-array and intra-array information (Healy and Hurly 1998). When the array of widely spaced flowers (>0.40 m) was shifted one spacing unit, the birds tended to return to the actual spatial location of the rewarded flower based on the extra-array cues. However, when the flowers in the array were more densely spaced (<0.40 m), hummingbirds returned to the correct flower position relative to the other flowers in the array. The results of the current experiments with squirrels seem to resemble the “wide spacing” situation in hummingbirds.

The results obtained in experiments 1–4 suggested that ground squirrels ignored local landmarks and attended preferentially to global cues or a familiar route to the goal. Since animals often approached food from their preferred burrows, the route was expected to play an important role in navigation. It seems unlikely, however, that memory of a familiar route alone provided squirrels with sufficient information to locate the food platform. In the 90° Turn experiment, less than half of the animals picked the correct platform, in spite of the fact that a familiar route was still present. Interestingly, platform #3 received more visits than any other “incorrect” platforms. If animals had relied only on a familiar route, they should have gone to platforms #4 or #5, because the ladder of platform #5 during the 90° Turn experiment was the closest to the position of platform #4’s ladder during training. The fact that four animals chose platform #3 instead suggests that squirrels may also have relied on local landmarks within the array, such as the log. In contrast, in the Parallel Shift experiment more “incorrect” squirrels visited platform #5, indicating that animals referred to the information provided by both, the log and the ball, and/or platforms’ arrangement. The selective attention only to the log in the 90° Turn experiment is puzzling. Perhaps, in the 90° Turn experiment the log was given more weight because it remained very close to the training position while the ball and platforms (except platform #4) were in the new location due to the nature of

rotation. On the other hand, in the Parallel shift experiment the whole array was in the completely novel location.

The results of the 90° Turn and the Parallel Shift experiments demonstrated that animals attended to the multiple types of cues. In the presence of familiar global landmarks (experiments 1–4) it appeared as if squirrels completely ignored local features of the array. However, when the appearance of global landmarks was manipulated (experiments 5–6), and it became obvious that subjects also encoded some information about local features of the array. The squirrels’ ability to find the correct platform was significantly lower on the last two tests, indicating that orienting with the help of proximal cues was a secondary mechanism. The extent to which the squirrels relied primarily on global landmarks as opposed to a familiar route remains unclear. However, the fact that performance on the 90° Turn (where the route was present) and the Parallel Shift (where the route was absent) experiments were similar suggest that squirrels used global landmarks as a primary mechanism. Relatively poor performance in experiments 5 and 6 could be also attributed to the fact that animals found the new arrangement of local landmarks disruptive. However, squirrels did not appear to behave any differently before or when approaching the array during these experiments compared to the first four experiments.

It is possible that in some cases ground squirrels rely on olfactory cues to locate their food. However, odor cues are unlikely to be consistently reliable in this habitat, which is subject to high, frequently fluctuating wind. In addition, even under favorable conditions squirrels must use other mechanisms for locating a food patch when approaching it from far away. In the present experiments, squirrels did not depend on food odor to locate the correct platform, since all the platforms contained oat shells. In experiments 1–4 food was present on two platforms. However, none of the animals went to the baited platform that was in the “incorrect” position with respect to global landmarks. If squirrels had used olfactory cues, at least some of them should have visited the second baited platform. In addition, the fact that in the 90° Turn and Parallel Shift experiments more than half of the animals missed the correct platform suggests again that olfactory cues are not the primary mechanism of orientation in this case.

How animals utilize available landmarks can vary from one sex to another (Williams and Meck 1993). Whether male Columbian ground squirrels navigate in the same way as females is not known, since only females were used in this study. The observed behavior of female ground squirrels was similar to what was reported for female rats that they also paid attention to both local and distant cues in their environment (Williams and Meck 1993). Moreover, the present experiments took place during gestation and lactation periods. As was shown previously with rats and meadow voles, a hormonal state of an animal can have an effect on navigational abilities and mechanisms used (Gaulin 1993; Williams and Meck 1993). How the hormonal state of gestation and lactation affects navigation is not known. During this time females are nutritionally stressed and spend most of their time foraging when above

ground (Neuhaus and Pelletier 2001); as a result, they may be especially motivated to remember good foraging locations. Since local landmarks are not as reliable as global ones, it is not surprising that animals attend preferentially to global features. Further research is needed to investigate whether Columbian ground squirrel females and males utilize the same mechanisms of navigation, and how the hormonal state of the animals affects their navigational ability.

Overall, these experiments suggest that female Columbian ground squirrels rely on multiple types of cues when orienting towards a food source. Local landmarks are used only as a secondary mechanism of navigation, and are not attended to when a familiar route and known global landmarks are present. Further tests need to be done to investigate the relative importance of global landmarks and routes for navigation.

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References

- Alyan S, Jander R (1994) Short-range homing in the house mouse, (*Mus musculus*) stages in the learning of directions. *Anim Behav* 48:285–298
- Balda RP, Kamil AC, Grim K (1986) Revisits to emptied cache sites by clark nutcrackers (*Nucifraga columbiana*). *Anim Behav* 34:1289–1298
- Bennett ATD (1993) Spatial memory in a food storing corvid.1. near tall landmarks are primarily used. *J Comp Physiol A-Sens Neural Behav Physiol* 173:193–207
- Biegler R, Morris RGM (1996) Landmark stability: further studies pointing to a role in spatial learning. *Q J Exp Psychol Sect B-Comp Physiol Psychol* 49:307–345
- Bingman VP (1998) Spatial representation and homing pigeon navigation. In: Healy S (ed) *Spatial representation in animals*. Oxford University Press, Oxford, pp. 69–85.
- Brodbeck DR (1994) Memory for spatial and local cues a comparison of a storing and a nonstoring species. *Anim Learn Behav* 22:119–133
- Cheng K (1989) The vector sum model of pigeon landmark use. *J Exp Psychol-Anim Behav Process* 15:366–375
- Cheng K, Spetch ML (1998) Mechanisms of landmark use in mammals and birds. In: Healy S (ed) *Spatial representation in animals*. Oxford University Press, Oxford, pp 1–17.
- Chittka L, Geiger K (1995) Can honey-bees count landmarks. *Anim Behav* 49:159–164
- Collett TS, Cartwright BA, Smith BA (1986) Landmark learning and visuospatial memories in gerbils. *J Comp Physiol A-Sens Neural Behav Physiol* 158:835–851
- Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71:180–188
- Devenport JA, Devenport LD (1994) Spatial navigation in natural habitats by ground-dwelling sciurids. *Anim Behav* 47:727–729
- Festa-Bianchet M, Boag DA (1982) Territoriality in adult female Columbian ground squirrels. *Can J Zool* 60:1060–1066
- Fiset S, Dore FY (1996) Spatial encoding in domestic cats (*Felis catus*). *J Exp Psychol-Anim Behav Process* 22:420–437
- Fiset S, Gagnon S, Beaulieu C (2000) Spatial encoding of hidden objects in dogs (*Canis familiaris*). *J Comp Psychol* 114:315–324
- Gaulin SJC (1993) How and why sex differences evolve, with spatial ability as a paradigm example. In: Haug M, Whalen RE, Aron C, Olsen KL (ed) *The development of sex differences and similarities in behavior*. Kluwer Academic Publishers, Dordrecht, pp 111–130.
- Healy SD, Hurly TA (1998) Rufous hummingbirds' (*Selasphorus rufus*) memory for flowers: patterns or actual spatial locations? *J Exp Psychol-Anim Behav Process* 24:396–404
- Henderson J, Hurly TA, Healy SD (2001) Rufous hummingbirds' memory for flower location. *Anim Behav* 61:981–986
- Jacobs LF, Schenk F (2003) Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychol Rev* 110:285–315
- Jacobs LF, Shiflett MW (1999) Spatial orientation on a vertical maze in free-ranging fox squirrels (*Sciurus niger*). *J Comp Psychol* 113:116–127
- Leonard B, McNaughton BL (1990) Spatial representation in the rat: conceptual, behavioral, and neurophysiological perspectives. In: Kesner RP, Olton DS (eds) *Neurobiology of comparative cognition*. Lawrence Erlbaum, Hillsdale, NJ, pp 363–422.
- Menzel R, Brandt R, Gumbert A, Komischke B, Kunze J (2000) Two spatial memories for honeybee navigation. *Proc R Soc Lond Ser B-Biol Sci* 267:961–968
- Murie JO, Harris MA (1988) Social interactions and dominance relationships between female and male Columbian ground-squirrels. *Can J Zool-Rev Can Zool* 66:1414–1420
- Neuhaus P, Pelletier N (2001) Mortality in relation to season, age, sex, and reproduction in Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool-Rev Can Zool* 79:465–470
- Shettleworth SJ (1998) *Cognition, evolution, and behavior*. Oxford University Press, New York
- Suzuki K, Kobayashi T (2000) Numerical competence in rats (*Rattus norvegicus*): Davis and Bradford (1986) extended. *J Comp Psychol* 114:73–85
- Suzuki S, Augerinos G, Black AH (1980) Stimulus-control of spatial-behavior on the 8-arm maze in rats. *Learn Motiv* 11:1–18
- Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208
- Wallraff HG (2001) Navigation by homing pigeons: updated perspective. *Ethol Ecol Evol* 13:1–48
- Williams CL, Meck WH (1993) Organizational effects of gonadal hormones induce qualitative differences in visuospatial navigation. In: Haug M, Whalen RE, Aron C, Olsen KL (eds) *The development of sex differences and similarities in behavior*. Kluwer Academic Publishers, Dordrecht, pp 175–189.