

The Relative Importance of Global and Local Landmarks in Navigation by Columbian Ground Squirrels (*Spermophilus Columbianus*)

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In order to survive, small burrowing mammals need to remember the locations of escape burrows. Therefore, it is important to know what types of landmarks are used to aid navigation in the wild. The author tested the ability of free-ranging Columbian ground squirrels (*Spermophilus columbianus*) to locate escape burrows when local (e.g., vegetation pattern, local relief), global (e.g., forest edge, mountain outline), or both types of landmarks were obstructed. Results suggest that squirrels need both local and global landmarks of the environment for successful navigation, and that the upper portion of the horizon is especially important for orientation. Moreover, the lack of information from one type of landmark (local or global) cannot be completely compensated by the other type.

Keywords: landmark-based navigation, spatial memory, Columbian ground squirrels, *Spermophilus columbianus*, landmarks

When a distant goal such as a burrow or food source cannot be perceived directly by any means, animals may use some stable and recognizable feature of the environment—a landmark—to locate their goal. Under natural conditions, however, animals are often faced with an enormous number of objects that could potentially be used as landmarks. The predictive value of a potential landmark depends on its proximity to the goal, its stability in space and time, and its uniqueness. Landmarks such as rocks or tree limbs that are located close to the goal (local landmarks) may allow more precise encoding of a goal's location than more distant but prominent features of the environment such as tree lines or mountains (global landmarks; Cheng & Spetch, 1998). Local landmarks, such as rocks or logs, however, are often not unique, and the presence of other, similar objects may complicate navigation. In contrast, global landmarks may provide a more consistently reliable indicator of a goal's approximate location because they are observable from greater distances, stable, and more likely to be unique (Biegler & Morris, 1996).

The use of landmarks varies greatly across species; some animals demonstrate preference for local landmarks and others for

global landmarks (reviewed in Healy, 1998, and Shettleworth, 1998). Many animals appear to rely on both local and global features of the environment, and often the use of a particular set of landmarks depends on the experimental conditions. For example, extensive studies of the rat spatial orientation have shown that these rodents pay attention to a variety of cues, such as the geometry of a room and objects within and outside of a maze (Leonard & McNaughton, 1990). Moreover, the different sexes in rats appear to use landmarks differently (Williams & Meck, 1993).

Animals that rely on multiple types of landmarks may use them to generate distinctive representations of space known as sketch bearing, and integrated maps (Jacobs & Schenk, 2003). Animals can use global landmarks or some distributed gradient cues (e.g., odor, light) to establish a bearing map, which provides directional information about the goal. On the other hand, unique objects close to the goal can provide accurate information about distance and form a sketch map of a particular location. These two maps may then be combined to generate an integrated map, which ultimately enables animals to travel efficiently. Because bearing and sketch maps use different spatial information, one can explore the relative contribution of each type of landmark for navigation by manipulating its availability.

Columbian ground squirrels are of particular interest to studies of the relative importance of local and global landmarks because of their need to remember many burrow locations. These squirrels live in colonies on alpine and subalpine meadows and forage over areas as large as 2 ha in size. They have extensive burrow systems and, when threatened by aerial or terrestrial predators, they seek cover by going into underground burrows. The density of burrow entrances varies greatly, with an average of 12 ± 2.4 SE burrows/100 m². Although the exact number of burrow locations remembered by squirrels is not known, field observations suggest that squirrels are easily able to locate multiple escape burrows even when these are hidden by snow or vegetation. Moreover, memory for individual territories and burrows appears to be retained over years. Columbian ground squirrels are long-lived hibernating an-

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imals that tend to return to the same territories each year, even if they have hibernated in another part of the meadow (personal observation).

The classification of landmarks as either local or global is relatively straightforward in the case of Columbian ground squirrels. Even when sitting upright, the squirrels are no more than 30 cm tall. Because they inhabit flat meadow terrain, which is often covered by tall grass, squirrels are probably unable to see landmarks such as logs and rocks from distances of more than a few meters. In contrast, tree lines, mountains, and gorges are visible from most positions in the meadow and can, therefore, serve as global cues for approximate orientation.

I investigated the use of local and global landmarks by Columbian ground squirrels when locating escape burrows through a series of tests in which local, global, or both types of landmarks were systematically obstructed. Local landmarks were considered

to be features located within 1.5 m of the goal, including local relief and other burrows. A similar designation of local landmarks (1-m radius) was used in studies of Clark's nutcrackers (Gould-Beierle & Kamil, 1999). Prominent features on the horizon, such as the forest edge or mountains, were considered to be global landmarks. The removal of local landmarks was expected to impair a sketch map, whereas obstruction of global landmarks should have affected the use of a bearing map. Moreover, if squirrels were biased toward using a particular set of cues, the disruption of the other cues should not have affected their navigational abilities.

Escape Burrow Experiment

Squirrels were placed into a testing arena and confronted with a simulated predator attack under each of five conditions (Figure 1). In control trials (Test C), when all landmarks were available,

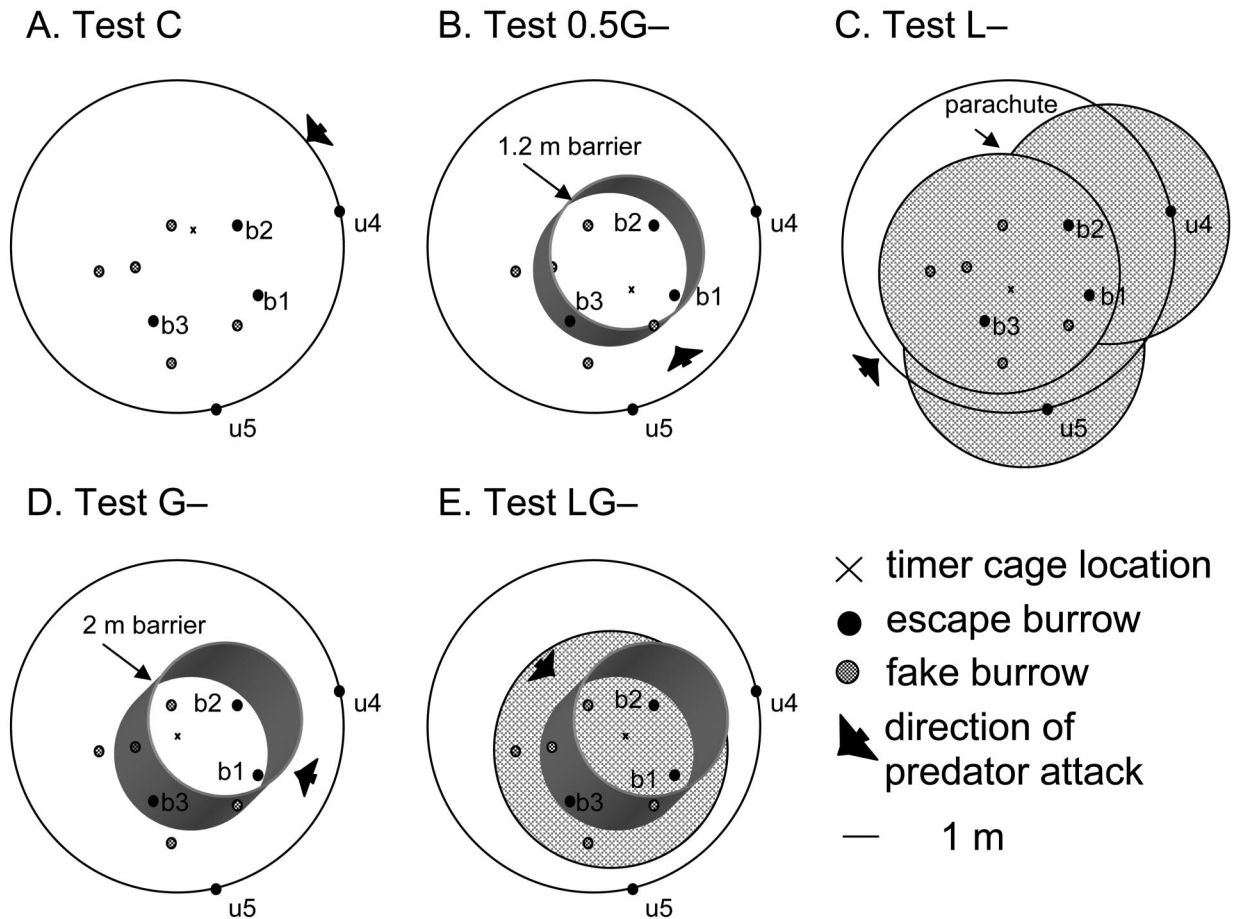


Figure 1. Escape burrow experiment: C, 0.5G-, L-, G-, and LG- tests. Diagrams depict the appearance of the testing arena (radius 5 m) on each of the five tests of the escape burrow experiment. A. Test C: All types of landmarks available. B. Test 0.5G-: Local landmarks present, global landmarks partially obstructed by a circular barrier (height 1.2 m, radius 2.3 m). C. Test L-: Local landmarks obstructed with parachutes (radius 3.5 m each) stretched over the surface of the ground in the arena, with a covered 1.5-m radius area surrounding each burrow; global landmarks present. D. Test G-: Local landmarks present, global landmarks obstructed with a tall barrier (height 2 m, radius 2.3 m). E. Test LG-: Local landmarks obstructed with a parachute (radius 3.5 m), global landmarks obstructed with a tall barrier (height 2 m, radius 2.3 m). b1–b3 = Burrows 1–3; u4–u5 = Underfence 4–5.

squirrels were predicted to run rapidly in the opposite direction of the predator to the closest burrow. In Test L–, when local landmarks were obstructed (impaired sketch map), the escape time was predicted to increase only slightly, because global landmarks were still present. By using their bearing map, squirrels could reach the general area of an escape burrow and then search within that area.

Test 0.5G–, when global landmarks were partially obscured and only the most prominent features remained visible, was predicted to lengthen escape time further. The increase in escape time should have been even more substantial on Test G–, when almost all global landmarks were obscured (impaired bearing map) and only cues from local landmarks were available. In this case, I predicted that squirrels would search throughout the arena until they stumbled over a set of familiar local landmarks. Finally, squirrels were expected to be most disoriented in the LG– test, when both local and global landmarks were unavailable. The escape time on Test G– should have been shorter than on Test LG– if squirrels could extract information from local landmarks when global landmarks were not available. In all five conditions, I predicted that squirrels would run in the opposite direction of the predator. Thus, although the choice of an escape burrow in the last three tests should almost have been random, subjects were still expected to search in a direction away from the predator. Comparison of escape times and locations among these five tests was predicted to reveal the relative importance of local and global landmarks for navigation.

In this experiment I chose to obstruct the view of various landmarks instead of introducing a specific landmark artificially and then manipulating it. The exact landmarks that squirrels attend to in either local or global categories are not known. Therefore, manipulating only a particular landmark in each category might not have revealed the overall importance of local and global landmarks.

Method

Subjects

I studied Columbian ground squirrels (*Spermophilus columbianus*) on a 1.5-ha subalpine meadow that was surrounded by pine and spruce forest and a road along the Gorge Creek drainage, in Alberta, Canada (50° N, 110° W; elevation 1,500 m). At the time of the experiment, the study population had been monitored for more than 5 years and included 102 adults. Squirrels were habituated to human observers and to regular trapping and marking. Squirrels could be repeatedly recaptured if necessary. All squirrels in the population were tagged on both ears with individually numbered tags (Monel #1, National Band and Tag Co., Newport, KY) for permanent identification. In addition, unique black marks were applied on the fur of each individual with hair dye (Lady Clairol Hydrience black opal; Clairol Inc., Stamford, CT) for easy identification from a distance.

Experiments were conducted in June–July 2004. At this time of the year, females could reliably be found within their territories (Festa-Bianchet & Boag, 1982; Murie & Harris, 1988). Because males did not hold territories at this point in the season and were difficult to locate regularly, only females were used.

Twenty females that resided on the main part of the meadow were chosen as subjects for the escape burrow experiments. One of these subjects disappeared before all of the experiments were completed.

Seventeen participating females were lactating when the experiment was conducted. Three other females did not breed that year. The reproductive status of the females was determined based on behavioral observations and trapping data. The exact estrus day was recorded for each female during the

mating period. Later in the season, the squirrels' nipples were examined during trapping to check whether they were lactating or not.

Testing Arena

The testing arena was set up by fencing with poultry netting an area of 5-m radius located in the center of a small meadow connected to the larger meadow where the colony of ground squirrels resided. The vegetation in the arena remained short (~0.1 m) throughout the experiment. One small log (0.6 m long) was present in the arena, but there were no bushes or rocks. The nearest tree stood 17 m away from the arena, but the majority of trees were at least 30 m away. There were no natural burrows present in the arena, and no squirrels resided within it. Three escape burrows within the arena and two underfence tunnels were dug, and subjects were trained to use them (see Figure 1). Originally, the escape burrows were 0.5 m deep and 0.12 m in the diameter. However, during the training period, squirrels enlarged these burrows extensively, and the lengths of all burrows exceeded 1.5 m at the time of the tests. The width of the burrows remained the same, and it was similar to the natural escape burrows. Underfence tunnels were represented by shallow trenches leading from one side of the fence to the other. When necessary, these tunnels could be closed with doors made of poultry netting.

In addition to the escape burrows, five 0.15-m deep, 0.12-m wide fake burrows were created by lifting up the upper portion of the turf. The resulting holes were filled halfway with scented soil created by mixing soil collected from the natural burrows of all 20 participating squirrels on the day of the test. These fake burrows provided a control for the use of burrow odor during escape. Fake burrows were available only at the time of the tests but not during training. At the end of each testing day, the scented soil was removed and the turf restored to its original place, so that squirrels were never exposed to fake burrows except during tests. If squirrels were relying primarily on olfactory or visual cues directly associated with a burrow, they were not expected to discriminate between fake and real burrows. The locations of fake burrows were concealed between tests to prevent squirrels from seeing (through the fence) and learning the locations of these burrows. The positions of the escape and fake burrows in the arena are shown in Figure 1.

Training

During training, each subject was captured within her territory and transported to the arena, where she was released into one of the artificial burrows. At this time the underfence tunnels were closed. Horse feed (Equisine Sweet Show Horse Ration, (Unifeed, Okotoks, Alberta, Canada), consisting primarily of oats and barley and supplemented by the addition of dry corn and pellets), which squirrels readily consume, was sprinkled in the arena to encourage exploration of the area after the squirrel emerged from the burrow. After exploring the arena for approximately 5 min, the squirrel was approached by a human observer until it escaped into one of the burrows. The human then moved away, and the squirrel was allowed to leave her burrow and continue to forage. The procedure was repeated until the squirrel used all three burrows. The use of a particular burrow was achieved by changing the direction of the human's approach and sprinkling horse feed only in certain areas of the arena. Squirrels were also observed to use escape burrows in the arena when natural alarms were heard. A training session lasted 15 min. At the end of the training session, the underfence tunnels were opened and the subject was encouraged to leave the arena by these routes and return to her territory. When the human approached from a direction opposite that of an underfence tunnel, the squirrel left the arena. However, if the squirrel failed to leave voluntarily, she was trapped and returned to her territory. On average, each squirrel received one training session per day for 30 days. At the end of the training, all participating squirrels regularly came to the arena area on their own and tried to enter it. These visits were controlled by closing and opening

underfence tunnel doors. If a squirrel scheduled for the training on that day was seen in the arena area, the underfence tunnel was opened to let her inside and then closed for the duration of the training. Unwanted squirrels were excluded from the arena by keeping underfence tunnels closed. The arena visits were controlled throughout the active day of the squirrels. At night, the tunnels were left open to prevent any nocturnal inhabitants of the meadow from being trapped in the arena.

Before the onset of the tests, subjects were also familiarized with a parachute and a barrier that were later used to obstruct local and global landmarks, respectively. To accustom the squirrels to the parachute, I stretched a parachute over the ground on each squirrel's territory. Diagonal slits forming an X were made in the parachute over the natural burrows, so squirrels could enter them. The parachute was pinned down to the ground by the large nails. Horse feed was sprinkled on the surface of the parachute to encourage a squirrels to walk on it and to enter burrows by holes when an observer approached. Squirrels were presented with the parachute five times for 30 min each time during the month of arena training. All squirrels readily walked across the parachute and entered burrows from the parachute's slits from the first session.

To familiarize squirrels with the barrier, I set up a barrier of 2.3 m radius and 0.5 m height around a squirrel's burrow. The barrier was made out of beige fabric wrapped around extendable metal poles. Horse feed was sprinkled inside the barrier to encourage squirrels to explore the enclosed area after they emerged from their burrows. Although many squirrels gave alarm chirps when first exposed to the barrier, all soon ignored it (stopped chirping) and moved freely in the enclosed area. After 30 min, I raised the barrier's height to 1.2 m. During the second session, the barrier was also raised to the height of 2 m. During the following three sessions, squirrels were presented only with the 1.2-m and 2-m high barriers. In the final session (Session 6) squirrels were enclosed only with the 2-m high barrier. When the barrier was not used for the individual familiarization, it was set up at the 2-m height at the different parts of the meadow near the territories of the participating squirrels. The barrier was always visible to all of the squirrels from any part of the meadow. Familiarizing sessions were conducted throughout the month of the arena training.

Testing

After the month-long training, squirrels were subjected to the five tests. Before each test, a subject was caught on her territory using a Tomahawk live trap (Tomahawk, WI) baited with peanut butter. The trap was then put into a pillowcase and transported to the test arena. All squirrels were exposed to the same duration of walking during transportation, the time it took to bring a squirrel from the furthest part of the meadow. As a result, all squirrels were expected to have similar levels of disorientation as a result of transportation regardless of whether they were caught relatively close to or far away from the arena.

Before release, the pillowcase-covered trap was placed on a turntable and rotated (6 rotations at 12 rpm). After rotation, the squirrel was transferred to a timer cage ($0.3 \times 0.3 \times 0.3$ m) within the arena. The squirrel could see through the wire mesh of the lower part (0.15 m) of the timer cage. The upper portion of the cage was covered with a lid made out of nontransparent hard plastic with a timer mechanism attached underneath. The location of the timer cage within arena was unique in each test (see Figure 1). After 1 min, a small door on top of the cage automatically slid open. As soon as the squirrel jumped on top of the cage, an aerial predator attack was simulated to motivate the squirrel to run to an escape burrow. A raptor model was thrown toward the squirrel from a height of 3 m by the experimenter positioned on the stand placed outside of the arena fence (for the tests in which global landmarks were available) or just outside of the barrier (for the tests in which global landmarks were obstructed). The predator model consisted of brown fabric stretched over a kite frame (wingspan 0.68 m, length 0.50 m), with a weight (sack of beans) added to the center. When thrown, the predator model glided into the arena. Squir-

rels were habituated to the observers on the stands and ignored them during training. However, squirrels reacted very strongly to the predator model thrown from a stand. The direction from which the predator was thrown was unique for each test (see Figure 1).

Squirrels were released in the arena under five different testing conditions described next.

Test C: Local and global landmarks present. During this control test, all natural landmarks, local and global, were available to the squirrels (Figure 1A).

Test 0.5G-: Local landmarks present, global landmarks partially obstructed. To partially block the view of global landmarks, a circular fabric barrier (height 1.2 m, radius 2.3 m) was constructed in the center of the arena. The barrier was pinned down to the ground with nails. From the squirrel's perspective on top of the cage (approximately 0.4 m from the ground), this barrier blocked the view of the meadow and the lower part of the trees on its edge. The upper part of the tree canopy was still visible to squirrels. Local landmarks within the barrier were available to the squirrels (Figure 1B).

Test L-: Local landmarks obstructed, global landmarks present. Local landmarks were covered with green parachutes (radius 3.5 m) stretched over the ground in the arena. Parachutes were arranged in such a way that an area of at least 1.5-m radius around each escape burrow or underfence tunnel was covered (Figure 1C). Diagonal slits forming an X were made over each burrow so that squirrels had potential access to them, but visual cues surrounding burrow entrances were obscured. To preclude the possibility that holes in the parachute might be associated with burrow entrances, there were also additional holes in the parachute that led either nowhere or to fake burrows. On the surface, all holes appeared indistinguishable to human observers. The parachutes were secured on the ground with long nails spaced at 0.5-m intervals. Grass under the parachutes pinned down by the nails created a surface different from the natural relief. In addition, two folded parachutes were placed under the top parachutes to modify local relief even further. To prevent squirrels from using olfactory trails that could be potentially left on the parachutes by previous participants, top and bottom parachutes were switched between trials. At the end of the day, parachutes were soaked and rinsed. In addition, parachutes were positioned differently from the previous day by rotating them about their centers.

Test G-: Local landmarks present, global landmarks obstructed. Global landmarks were obstructed by constructing a barrier in the arena as described in Test 0.5G- but taller (height 2 m, radius 2.3 m). The only global landmarks that squirrels could see were the very tips of two trees (~0.1 m). Local landmarks within the barrier were available to the squirrels (Figure 1D).

Test LG-: Local landmarks obstructed, global landmarks obstructed. Local landmarks were obstructed as in Test L-, and global landmarks were obstructed as in Test G-. All global cues except the very tips of two trees (~0.1 m) were unavailable. In addition, the squirrels could not see any local landmarks on the ground because the parachute was concealing them. As in Test L-, the parachutes were rotated between each test (Figure 1E).

To prevent squirrels from using some features of the testing environment as a reference point, the positions of the supporting poles for the barrier in Tests 0.5G-, G-, and LG- were different on each test.

All squirrels were subjected first to Test C to establish whether they knew the position of the artificial burrows. To eliminate the effects of learning, the order of the other four tests was randomly assigned to each squirrel from 24 possible combinations. In most cases, each squirrel was tested every other day. Each test lasted until the subject found an escape burrow. All trials were videotaped using a Cannon ZR-65 camcorder (Canon, Tokyo, Japan). Later these recordings were analyzed using Adobe Premiere Pro software package for the location and the duration of the escape. The following information was extracted from the tapes: the time it took a squirrel to enter an escape burrow once she jumped off the timer

cage, the burrow she escaped into, and whether a squirrel paused by any of the fake burrows.

Nonparametric tests were chosen for the analysis of the squirrel escape times, because the original data did not satisfy the normality assumption, and logarithmic transformation was not successful (two-tailed Kolmogorov–Smirnov test, $Z = 1.851$, $p < .002$). Friedman and Wilcoxon’s signed-ranks tests (Siegel & Castellan, 1988) were used to compare squirrel escape times under different conditions (C, 0.5G–, L–, G–, and LG–). Effect size (d) was calculated as ratio of D over s , where D was the mean difference between the paired observations and s was standard deviation. Sequential Bonferroni correction was applied to control for multiple comparisons (Sokal & Rohlf, 1995). Chi-square tests were used to analyze the burrow choice on different tests.

Results

Squirrels successfully learned the positions of artificial burrows, and on Test C all individuals escaped into burrows within 3 s ($Mdn = 2.00$, interquartile range [IQR] = 0.00). The escape time for the other tests varied greatly (0.5G–: $Mdn = 2.00$, IQR = 4.00; L–: $Mdn = 4.00$, IQR = 4.00; G–: $Mdn = 5.50$, IQR = 11.75; LG–: $Mdn = 8.00$, IQR = 21.00; Figure 2). Squirrels either escaped directly (shorter escape times) or first ran in the wrong direction before turning and finding an escape burrow (longer escape times). In some cases, squirrels appeared completely disoriented and made multiple stops and turns before reaching a burrow.

How long it took squirrels to reach an escape burrow depended on the types of landmarks available to them: Friedman test, $\chi^2(4, N = 16) = 19.52$, $p < .001$. When local landmarks were available and global landmarks only partially obstructed, subjects’ escape times did not differ from their times during control trials (one-tailed Wilcoxon’s signed-ranks test, C vs. 0.5G–: $Z = -1.54$, $N =$

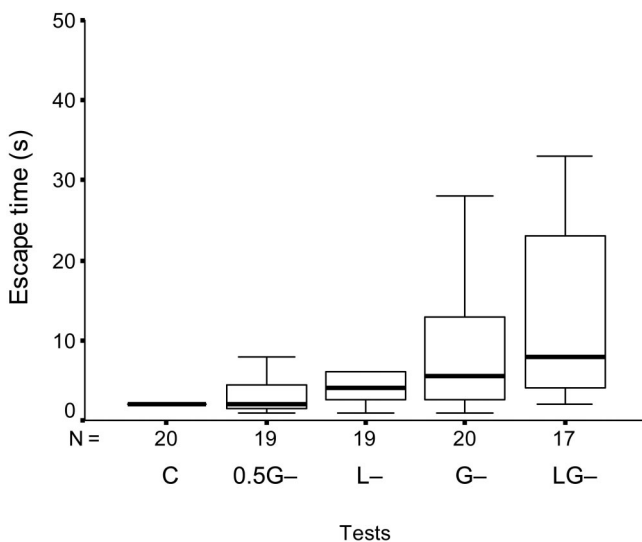


Figure 2. Squirrel escape time during C, 0.5G–, L–, G–, and LG– tests. Boxplots show medians and interquartile ranges. Numbers under x -axis indicate number of animals that completed the test. C = all types of landmarks present (control test); 0.5G– = local landmarks present, global landmarks partially obstructed; L– = local landmarks obstructed, global landmarks present; G– = local landmarks present, global landmarks obstructed; LG– = local and global landmarks obstructed.

19, $p = .062$, $d = 0.76$). However, when local landmarks were obstructed but all global landmarks remained, subjects’ escape times increased significantly (one-tailed Wilcoxon’s signed-ranks test, C vs. L–: $Z = -2.90$, $N = 19$, $p < .002$,¹ $d = 0.57$). Similarly, when global landmarks were almost entirely removed, subjects’ escape times also increased significantly, even though local landmarks were still available (one-tailed Wilcoxon’s signed-ranks test, C vs. G–: $Z = -3.13$, $N = 20$, $p < .001$ [see footnote 1], $d = 0.84$). Indeed, subjects’ escape times under this condition were significantly longer than when global landmarks were only partially obstructed (one-tailed Wilcoxon’s signed-ranks test, 0.5G– vs. G–: $Z = -2.73$, $N = 19$, $p = .003$ [see footnote 1], $d = 0.83$). Finally, and not surprisingly, when both local and global landmarks were unavailable, subjects’ escape times were considerably longer than under control conditions (one-tailed Wilcoxon’s signed-ranks test, C vs. LG–: $Z = -3.24$, $N = 17$, $p < .0005$ [see footnote 1], $d = 1.06$). Squirrels’ performance on L– and G– tests was similar (one-tailed Wilcoxon’s signed-ranks test, L– vs. G–: $Z = -0.52$, $N = 19$, $p = .301$, $d = 1.03$).

Although some subjects appeared to make use of local landmarks when locating escape burrows, their presence alone did not improve performance when global landmarks were unavailable (one-tailed Wilcoxon’s signed-ranks test, G– vs. LG–: $Z = -1.01$, $N = 17$, $p = .156$, $d = 1.03$). Similarly, the presence of global landmarks alone did not improve escape time compared with the condition in which all landmarks were unavailable (one-tailed Wilcoxon’s signed-ranks test, L– vs. LG–: $Z = -1.92$, $N = 17$, $p = .0275$,² $d = 1.31$).

The order in which squirrels received 0.5G–, L–, G–, and LG– tests did not affect their performance on these tests: Friedman test, $\chi^2(3, N = 16) = 1.02$, $p < .795$.

Contrary to my prediction, squirrels did not seem to escape to the closest burrow in the direction away from the predator (Table 1). There was no evidence that squirrels preferentially escaped into a particular burrow on Tests C, 0.5G–, and G–: C, $\chi^2(2, N = 20) = 4.90$, $p > .086$; 0.5G–, $\chi^2(2, N = 19) = 2.00$, $p > .368$; G–, $\chi^2(2, N = 17) = 1.88$, $p > .390$. On Test LG–, however, squirrels did appear to differentiate among burrows, $\chi^2(2, N = 15) = 10.00$, $p < .007$. In this test, squirrels escaped into either Burrow 1 or 3 but completely avoided Burrow 2. In Tests C and L–, squirrels had an access to the underfence tunnels in addition to the escape burrows. However, the use of the tunnels was very different in the two tests (McNemar test, $N = 18$, $p = .008$). In Test L–, 44% of squirrels tried to escape using underfence tunnels, but none chose them on Test C. Because of a small sample size, it could not be established whether squirrels preferred a particular burrow or tunnel for the escape on Test L–, but none went to Burrow 3.

Whether individual preferences for a particular burrow exist could not be resolved, because each individual was tested only five times. However, it should be noted that none of the squirrels consistently escaped into the same burrow on all the tests (Table 2).

Squirrels, for the most part, tended to ignore fake burrows. Only 1 squirrel on Test G– first attempted to escape into one.

¹ This probability value retained its significance after applying the sequential Bonferroni correction for multiple tests.

² The probability value of .0275 does not retain its significance after application of sequential Bonferroni correction.

Table 1
Proportion of Squirrels Choosing Burrow 1 (b1), Burrow 2 (b2), Burrow 3 (b3), Underfence Tunnel 4 (u4), and Underfence Tunnel 5 (u5) on C, 0.5G-, L-, G-, and LG- Tests

Burrow	Test				
	C	0.5G-	L-	G-	LG-
b1	0.45	0.21	0.11	0.18	0.33
b2	0.10	0.47	0.45	0.41	0
b3	0.45	0.32	0	0.41	0.67
u4	0	—	0.33	—	—
u5	0	—	0.11	—	—

Note. Underfence tunnels were not available to squirrels on 0.5G-, G-, and LG- tests. C = all types of landmarks present (control test); 0.5G- = local landmarks present, global landmarks partially obstructed; L- = local landmarks obstructed, global landmarks present; G- = local landmarks present, global landmarks obstructed; LG- = local and global landmarks obstructed.

Discussion

Results suggest that squirrels relied on both local and global features of the environment for successful navigation. The lack of information from one type of landmark could not always be compensated for by the other type. The short escape times on Test C demonstrated that squirrels can successfully learn to use new escape burrows. Removal of local (Test L-), global (Test G-), or both types (Test LG-) of landmarks affected the ability of squirrels to find escape burrows quickly (see Figure 2). However, squirrels' ability to find escape burrows was not affected if only the lower portion of horizon was obstructed. Squirrels did not consistently escape to the closest burrow in the direction away from a predator.

Overall, the results of this study support the idea that squirrels use both bearing and sketch maps; however, there appears to be considerable variation among individuals in the relative importance assigned to each mapping system. Much of the variation in performance across test types was due to individual differences in escape behavior. Some squirrels had shorter escape times than others when any types of landmarks were obstructed. When this is taken into account by comparing performance of each squirrel across the tests, it also becomes apparent that some squirrels took relatively longer to escape when local landmarks were available, whereas others took longer when global landmarks were available. This selective preference for local or global landmarks by different squirrels is currently being investigated.

Although local landmarks are important for indicating exact distance to and position of the goal (Biegler & Morris, 1996; Cheng, 1990; Jacobs & Schenk, 2003), global landmarks may also provide this type of information. For example, Clark's nutcrackers can find their goal quite accurately even in the absence of local landmarks (Gould-Beierle & Kamil, 1999). In Columbian ground squirrels, certain individuals were also able to find the location of the burrow very quickly without any help from local landmarks (Test L-), suggesting that they knew exactly where to search. Potential global landmarks were relatively far from the burrows. At the test location the closest trees were 17 m away, but the majority of the trees stood at least 30 m away. Moreover, a few squirrels were able to locate burrows very quickly even when both

local and global landmarks were eliminated (Test LG-). The obstruction of global landmarks made most of the visual cues unavailable except for the tips of two trees. Perhaps even this impoverished cue was sufficient for successful orientation. Short escape times of some squirrels could also be attributed to the use of other information such as auditory cues. Squirrels could have used noises coming from the main meadow or forest edge to aid their orientation.

The squirrels' performance in Test 0.5G- was similar to that in the control condition (C), indicating that seeing only a portion of the global landmarks was sufficient for successful orientation. When most of the global landmarks were obstructed (Test G-), the escape time increased dramatically. The usefulness of the cues in the upper portion of the horizon is not surprising, because these cues are the most prominent and reliable features of the environment. At the end of the summer, the grass on the study meadow is very tall (> 1 m), and any animals that rely on the information provided by the lower portion of the horizon will be at a disadvantage. In addition, occasional spring snowstorms can cover the meadow with a few feet of snow, but ground squirrels dive into the snow precisely at burrow openings (personal observation). Other animals, such as Clark's nutcrackers, also show preference for tall objects when orienting themselves (Gould-Beierle & Kamil, 1996, 1999). A test addressing the importance of the lower portion of the horizon for navigation was attempted. However, wind presented logistical difficulties, and this test was not performed.

Previous work on Columbian ground squirrels showed that, when searching for food in an array of feeders, squirrels rely on

Table 2
Squirrel Choice of Burrow 1 (b1), Burrow 2 (b2), Burrow 3 (b3), Underfence Tunnel 4 (u4), or Underfence Tunnel 5 (u5) on C, 0.5G-, L-, G-, and LG- Tests

Subject	Test				
	C	0.5G-	L-	G-	LG-
1	b3	b1	u4	—	—
2	b2	—	b2	b1	b1
3	b2	b2	u4	—	b3
4	b3	b2	b2	b3	b3
5	b3	b3	—	b3	b1
6	b1	b1	b2	b3	b1
7	b3	b2	b2	b2	b3
8	b3	b1	b1	b2	—
9	b3	b1	b1	b2	b3
10	b3	b3	u4	b1	—
11	b2	b2	u4	b2	b3
12	b2	b3	u4	b3	b3
13	b2	b2	b2	b2	b3
14	b2	b3	u5	b3	b3
15	b2	b2	b2	b1	b1
16	b2	b2	b2	b2	b3
17	b2	b2	u5	b3	b1
18	b3	b3	—	b2	—
19	b1	b3	b2	b3	—
20	b3	b2	u4	—	b3

Note. C = all types of landmarks present (control test); 0.5G- = local landmarks present, global landmarks partially obstructed; L- = local landmarks obstructed, global landmarks present; G- = local landmarks present, global landmarks obstructed; LG- = local and global landmarks obstructed.

global landmarks and use local landmarks only when known global information is not available (Vlasak, 2006). However, as seen from the present experiment, to find an escape burrow squirrels need information from both local and global landmarks. This difference could be due to the distinct testing procedures. During the foraging experiments, the information provided by local and global landmarks was in conflict, whereas during the escape burrow experiment one set of cues was simply eliminated. Alternatively, if different individuals tend to use different strategies of navigation, then the outcome depends on the type of individuals tested. Finally, it is possible that food and burrow locations are encoded differently by squirrels, or the time pressure associated with escape may increase the importance of local landmarks for orientation.

In Tests C, 0.5G-, and G-, there is no indication that squirrels preferentially escaped into a particular burrow. This could be due to the fact that three burrows were relatively close to the release sites, and squirrels did not perceive a difference in the distances traveled as being essential (M difference in distance to a burrow = 0.77, $SD = 0.54$). In these three tests, the direction of a predator attack also did not seem to have a dramatic effect on burrow choice, and in a few cases squirrels even escaped into burrows that were in the direction of a predator attack (Test C, Burrow 2; Tests 0.5G- and G-, Burrow 1; see Table 1).

In Tests L- and LG-, squirrels seemed to avoid certain burrows. For example, Burrow 3 in Test L- was avoided by all squirrels, perhaps because it was in the direction of a predator attack even though it was closest to the release site (Figure 1C). The reason for avoidance of Burrow 2 in Test LG- is unclear. Some squirrels used underfence tunnels on Test L- but none on Test C. Underfence tunnels were further from the release sites than any of the burrows, and they did not provide safety. Potentially, squirrels could only pass through them to exit the arena, and then they still would have to run a considerable distance (> 10 m) to reach a natural burrow. In addition, squirrels had encountered closed tunnels during training (tunnels were closed during the tests as well). All of this indicates that tunnels were a less optimal escape option than burrows; therefore, it is not surprising that they were avoided in the control test. Nonetheless, when local landmarks on the ground were obstructed, some squirrels went for the tunnels, perhaps using the fence to guide them.

It is important to note that only females were used in this study. As a result, it remains to be determined whether males use landmarks in a similar way. Laboratory studies on rats have demonstrated that males and females use visuospatial cues differently: Males tend to rely only on distal cues such as geometry of the experimental room, but females use both geometry of the room and landmarks (large objects in the room) when performing maze tasks (Williams & Meck, 1993). Although it is difficult to compare laboratory and field studies, my experiments with Columbian ground squirrels also show that females rely on multiple types of cues in the natural, wild environment.

The hormonal state of an animal can affect its navigational skills as well. For example, male meadow voles perform better relative to females on spatial tasks during the breeding season, but these differences become less pronounced during the nonbreeding period (Gaulin, 1993). Seventeen of 20 participating ground squirrel females in the present study were lactating when tests were conducted. Because the need to find escape burrows persists beyond

the breeding season, it seems unlikely that females would perform differently when in other reproductive states. However, this question needs to be further investigated.

Many animals are known to use other mechanisms in addition to landmarks when navigating (Collett & Graham, 2004; Etienne, Maurer, & Seguinot, 1996; Wehner, Michel, & Antonsen, 1996). It is likely that, under natural conditions, squirrels use path integration or route-based orientation to supplement information provided by landmarks. When animals use path integration, they continuously keep track of the changes of their position in space with respect to a particular location. Under the current experimental conditions, squirrels were unable to use this method of navigation because the transportation to and rotation within the arena eliminated any internal sense of direction. Similarly, squirrels could not rely on a known motor routine of getting from one place to another. There were no established routes from the release sites to the burrows, because squirrels were released from a new location on each test.

In this experiment, subjects' performance did not appear to be aided by olfactory cues, because such cues were either not present (no olfactory trails) or did not provide reliable information (fake burrows). Squirrels were released from a different location on each test and, therefore, could not have followed established odor trails even on the tests in which ground was not covered with parachutes. Because tests were conducted in a random order, on each given day squirrels were released from several locations, and a squirrel could not have used olfactory cues left by the previous participants. Also, because of the presence of fake burrows, squirrels could not have been guided to safety simply by the burrow odor. It seems possible that, at this study site, olfactory cues may generally be relatively unreliable, because the habitat is very windy, and wind direction often changes. In addition, during rapid escape squirrels may not have time to assess the gradient of a burrow odor. Further studies incorporating olfaction are necessary to investigate the importance of olfactory cues for squirrel navigation.

Although much is known about orientation in animals within a laboratory environment, relatively few studies have addressed questions of spatial memory and navigation in free-ranging mammals (but see Devenport & Devenport, 1994; Devenport, Luna, & Devenport, 2000; Jacobs & Shiflett, 1999; MacDonald, 1997; Manser & Bell, 2004). Field experiments, however, may permit a more precise evaluation of the relative importance of large-scale global landmarks and more immediate local landmarks for orientation. For example, numerous studies conducted in captivity have suggested that animals preferentially attend to global landmarks and often ignore information provided by local landmarks (Alyan & Jander, 1997; Brodbeck, 1994; Gould-Beierle & Kamil, 1996; Leonard & McNaughton, 1990; Suzuki, Augerinos, & Black, 1980). These studies, however, have been conducted in relatively confined quarters, with the result that landmarks identified as either global or local are separated by only a few meters. For example, Clark's nutcrackers were tested in a 4.40×2.70 -m room (Gould-Beierle & Kamil, 1996) and chickadees in a $2.45 \times 3.50 \times 2.27$ -m room (Brodbeck, 1994). In contrast, in the open meadows inhabited by Columbian ground squirrels, global landmarks such as tree lines or mountain ranges are often located at a great distance from the squirrels' burrows. Perhaps as a result, the

squirrels relied on both global (> 17 m) and local (< 1.5 m) landmarks when locating escape burrows in the present study.

Data from this experiment in conjunction with other studies suggest that animals are plastic in their use of landmarks. As mentioned, the relative importance of local and global landmarks for navigation during a foraging task was different. Similarly, field studies on hummingbirds showed that the use of local and global landmarks depended on how closely flowers were arranged in the testing array (Healy & Hurly, 1998; Hurly & Healy, 1996). Thus, animals appear to use landmarks differently under various circumstances.

Because of great selection pressure on Columbian ground squirrels to remember the locations of burrow entrances and the ability to do field tests on this species, these animals are especially valuable for studies of navigation. This experiment conducted controlled field tests demonstrating the importance of local and global landmarks for ground squirrel navigation. However, the exact features in the global and local environments animals attend to still remain known. Future field experiments in which animals are tested with artificially introduced landmarks of local and global scales that can be manipulated would help to understand the processes of orientation even further.

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