

Spatial Orientation on a Vertical Maze in Free-Ranging Fox Squirrels (*Sciurus niger*)

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To determine how squirrels return to remembered locations in an arboreal environment, wild fox squirrels (*Sciurus niger*) were trained on an outdoor vertical maze. Squirrels were trained on 1 route and tested with all routes accessible. Possible mechanisms of spatial orientation were distinguished with manipulations such as rotations, shifts, and blocked routes. Squirrels consistently used an extra-maze, allothetic frame of reference to orient and appeared to organize their memory of the route hierarchically. This study demonstrates that a laboratory technique, the maze, can be successfully brought into the field to measure mechanisms of spatial orientation under natural conditions in free-ranging wild rodents. Such studies will allow researchers to determine what kind of spatial information is acquired by wild animals under natural conditions and how this information is used.

The coding of space by the rodent has been at the heart of many controversies in comparative psychology, starting with the debate over place versus response learning (Hull, 1934; Tolman, 1948) and continuing in the debate over the role of the hippocampus in computing a cognitive map (Eichenbaum, Cohen, Otto, & Wible, 1992; Munn, 1950; Nadel, 1991; O'Keefe & Nadel, 1978; Olton, Becker, & Handelmann, 1979). Yet despite decades of study, determining precisely how rodents create maps of their environment is still controversial (McNaughton et al., 1996), perhaps because animals do not use a single mechanism or strategy but rely on multiple, redundant sets of cues for spatial orientation (Schöne, 1984; Wehner, Michel, & Antonsen, 1996). Cues used in spatial orientation range from the simple beacon that coincides with the goal, to local cues that are associated with a distance from the goal, to the incorporation of many cues into an external frame of reference within which a rodent may relate one object to another (Collett, Cartwright, & Smith, 1986). The frame of reference may be of two types: *ideothetic* (i.e., egocentric), in which positions

are coded relative to the body position of the observer, and *allothetic* (i.e., allocentric), in which positions are coded only in relation to objects external to the observer (O'Keefe & Nadel, 1978; Schöne, 1984).

All cues are not used equally: In a heterogeneous environment, laboratory rats orient preferentially to an allothetic frame of reference (Suzuki, Augerinos, & Black, 1980). Moreover, the allothetic frame of reference is often defined primarily by distal landmarks, perhaps because they remain more constant compared with proximate objects (Bennett, 1993; Biegler & Morris, 1993; Hebb, 1949). Yet, evidence from behavioral and physiological studies indicates that laboratory rats code both proximal and distal cues simultaneously (Gothard, Skaggs, & McNaughton, 1996); it is simply the degree to which each is used that varies with the experimental situation. For example, laboratory rats solve the radial arm maze relative to distal landmarks and rotate their orientation if these landmarks are rotated. Yet if the cues are removed, rats switch to an ideothetic strategy (e.g., stereotyped turns) to solve the maze (Suzuki et al., 1980).

The spatial frame of reference used for orientation may also vary between species according to their ecology and developmental history. In general, food-storing bird species (e.g., black-capped chickadee [*Parus atricapillus*], marsh tit [*P. palustris*], and European jay [*Garrulus glandarius*]) rely on distal cues to orient to the location of a rewarded location, even in a bare laboratory aviary, whereas nonstoring species (e.g., dark-eyed junco [*Junco hyemalis*], blue tit [*P. caeruleus*], or jackdaw [*Corvus monedula*]) are as likely to orient to the feeder color as to its location (Brodbeck, 1994; Clayton & Krebs, 1994). Among species, developmental history can influence spatial ability in different ways. Marsh tits show enhanced spatial performance after enriched rearing; blue tits show no effect of developmental history on spatial strategy (Clayton, 1995). Even in humans, how we code the location of an object varies widely and unpredictably among cultures. Tzeltal-speaking participants from Tenejapa (Chiapas, Mexico) code objects in absolute space (i.e., the chair is north of the table), whereas Dutch

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participants code the same objects in relative space (e.g., the chair is to the left of the table; Levinson, 1996).

Thus, the mechanism by which an animal orients in space may differ according to species, developmental history, and experimental context. For this reason, it is critical to study the phenomenon under a range of experimental conditions. Studies of maze orientation in rodents have been solely based on laboratory-reared animals. Only one study has measured the use of outdoor cues (i.e., celestial cues; Kavaliers & Galea, 1994); there have been no outdoor maze studies in free-ranging rodents. It is also important to study a variety of species, because maze performance in rodents may differ according to a species's preferred means of locomotion: For example, the terrestrial laboratory mouse learns more slowly than the semi-aquatic laboratory rat in a water maze but not in a dry-land maze (Whishaw & Tomie, 1996). Likewise, a visually guided species (e.g., diurnal species, such as members of the gerbil [Gerbillinae] subfamily or squirrel [Sciuridae] family) may rely more heavily on visual landmarks and allothetic orientation than a nocturnal or fossorial species. Finally, arboreal species may orient in space differently than species that are primarily terrestrial (e.g., Grob ty & Schenk, 1992). The goal of the present study was to study spatial orientation in a natural setting, using free-ranging subjects of a highly visual and arboreal rodent species, the fox squirrel (*Sciurus niger*).

The natural foraging behavior of tree squirrels makes them ideal candidates for maze studies. Fox squirrels and gray squirrels (*S. carolinensis*) search for profitable patches of tree seeds in the canopy of the eastern deciduous forest (Armitage & Harris, 1982). A foraging squirrel must learn complex routes through the tree canopy to locate seeds. Because of the rapid harvesting of a food tree, the status of each food patch may change unpredictably over time, forcing a squirrel to find new patches and new routes. Once satiated, squirrels begin caching the acorns, hickory nuts, or walnuts by carrying one seed at a time to the forest floor (L. F. Jacobs, 1995); squirrels can then use spatial memory to relocate these caches (L. F. Jacobs & Liman, 1991). After caching, they return to the same tree and often to the same area of the canopy (L. Jacobs, unpublished observation, 1985).

Thus, the fox squirrel lives in a spatially complex, arboreal environment, where it must remember canopy locations. To determine what frame of reference free-ranging fox squirrels use to return to locations in this environment, we constructed an outdoor vertical maze, which mimicked the vertical structure of their foraging environment, and tested squirrels on their own home range, where a full array of familiar cues were available to them for orientation.

Squirrels could solve the maze using at least three types of strategies. First, they could associate certain odor cues, such as the odor of the bait or the odor of a scent trail on the correct route, with the reward and solve the maze by searching for these stimuli. Second, squirrels could use an ideothetic frame of reference, coding locations relative to their body movements and returning to the site by repeating a memorized sequence of movements (i.e., a response strategy). Third, the squirrels could use an allothetic frame

of reference, coding locations relative to the configuration of ladders within the maze (i.e., intramaze) or relative to external cues, such as trees (i.e., extramaze). Using three groups of squirrels in three campus locations, we distinguished between the use of these strategies by manipulating the maze with rotations, lateral shifts in space, and forced detours. On the basis of results from laboratory rodents and from our previous results on fox squirrels (Lavenex, Lee, Shiflett, & L. F. Jacobs, 1998), we predicted that fox squirrels would code the goal in reference to an external frame of reference on the basis of distal landmarks.

General Method

The vertical maze consisted of a parallel set of narrow ladders suspended from a high crossbar (Figure 1A). These vertical access

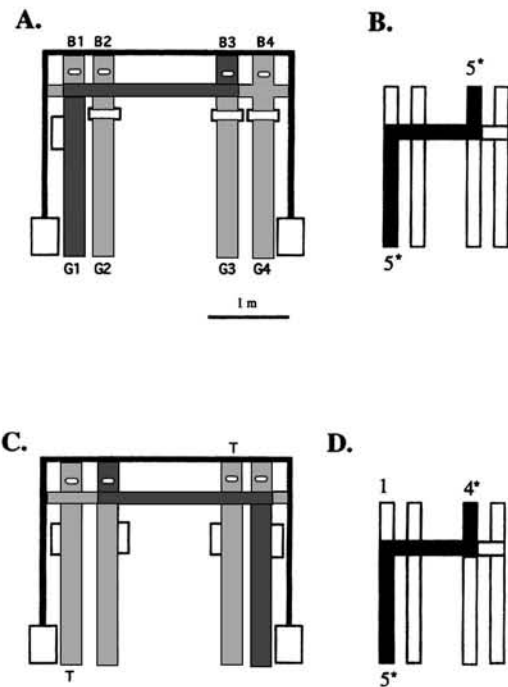


Figure 1. (A) Schematic drawing of the maze, shown during the unmanipulated test in Experiment 1. Two aluminum poles were held upright in two plastic buckets (shown as white rectangles) filled with concrete, from which black plastic ladders were suspended. The horizontal white rectangles indicate the position of the baffles; white circles represent bait cups. The scale is shown in meters. The ladders are numbered from left to right, as are their choice points (G = ground choice, B = branch choice). The darkly shaded ladders represent the training route (G1-B3) and hence the position of the training ladders during the unmanipulated test. (B) Results from the unmanipulated test, shown on a schematic drawing of the maze. Solid bar = location of route relative to extramaze cues (G1-B3). The number of squirrels choosing a ladder on their first trial is shown above or below each ladder ($*p < .05$). (C) Schematic drawing of the maze after rotation. The darkly shaded ladders represent the training route. Open baffles are represented by vertical white rectangles. The location of the training route relative to extramaze cues is marked with a "T" at the ground (G1) and at the end (B3). (D) Results from the rotation test; conventions as in Part B.

Table 1
Strategies for Spatial Orientation, Behavioral Consequences, and Experimental Manipulations

Strategy	Behavior	Manipulation	Experiment(s)
Beacon	Orient to bait	Remove bait	1, 2, 3, 4, & 5
Local cue	Orient to training ladders	Rotate maze	1, 2, 3, & 4
Ideothetic frame	Replicate turns	Shift maze	2 & 4
Allothetic frame	Orient to location relative to allothetic cues	Shift maze	2 & 4
Using intramaze cues	Use same route within maze	Shift maze	2 & 4
Using extramaze cues	Use same route relative to external cues	Shift maze	2 & 4
Using list of extramaze local views	Orient to key choice points	Remove choice point	5

ladders were connected by a horizontal ladder, leading to a second level of short ladders, one of which was baited with a peanut, which was similar to a trunk of tree leading to the branches of a tree. This created two choice points: at the "trunk" and the "branch." Squirrels were trained to climb a specific route to retrieve the reward; during test trials, the maze was manipulated to determine what cues the squirrels were using to return to the reward location. We used three types of maze manipulations (i.e., remove bait, rotate maze, shift maze) to distinguish between possible mechanisms of orientation. The possible strategies that could be used to solve the maze, their behavioral consequences, and the experimental manipulation that would distinguish the use of this strategy, are shown in Table 1.

To differentiate between these possible mechanisms, we conducted five experiments on three study sites. The design of the experiments and the order in which they were conducted are shown in Table 2. We ran the experiments in chronological order, and, thus, all squirrels were tested in the same order. No squirrel was tested on all experiments; on average, an individual squirrel participated in 2.4 ($SE = 1.3$) experiments (range = 1–4). Even though squirrels varied in their participation, testing them in the same order was unavoidable because of the time needed to rebuild the maze and train squirrels for each experiment. Also, we did not know if the same number of squirrels would appear at the site later in the season. Thus, we decided to test the maximum number that could be trained at a particular time and at a particular location.

Animals

The study animals for each experiment were drawn from a pool of 24 individually marked male and female fox squirrels (*Sciurus*

niger) on the Berkeley campus that were resident at our three study sites. These squirrels are members of the larger Berkeley population of this introduced species. Two individuals were judged to be subadult (<500 g), but all others were adult. Adult weight (>500 g) was confirmed for some animals. Each squirrel's sex was determined, and they were individually marked with black fur dye (Nyanzol, J. Belmar, Inc., North Andover, MA).

For each experiment, we tested all squirrels that had met our training criterion after approximately 3 weeks of training. A squirrel was only excluded from the experiment if it did not meet this criterion; otherwise, all trained squirrels that showed up during the testing period were included in the experiment. The squirrels that did not reach criterion appeared to be resident elsewhere, as they appeared less frequently and, hence, did not reach criterion at the same time (i.e., within 3 weeks) as more frequent visitors. Thus, we trained all the squirrels that appeared regularly at a study site; this number varied from 4 to 12, depending on the location, the time of year, and the length of time we had been provisioning that site. The number of squirrels generally increased as we continued testing on that site (e.g., Experiment 4 has more subjects than Experiment 3). However, by the end of the study, the squirrels had begun harvesting acorns. This alternate source of food appeared to reduce their motivation to be fed on the maze, and consequently the number of subjects decreased between Experiments 4 and 5.

Study Site

Testing took place over three sites within a grove of mature trees, consisting of bluegum eucalyptus (*Eucalyptus globulus*), redwood (*Sequoia sempervirens*), and coast live oak (*Quercus agrifolia*) on the University of California, Berkeley, campus. The study sites

Table 2
Design of Experiments

Experiment	Hypothesis(es)	Manipulation
Experiment 1	Squirrels orient either to a beacon or to local cues.	Remove bait, rotate 180°
Experiment 2	They orient either to an ideothetic or to an allothetic frame of reference.	Shift to right
Experiment 3	They will use local cues if the cues are more salient.	Train on orange route
Experiment 4 (1st configuration)	They will take the direct route if trained without baffles.	Train on 1 ladder, add 3 ladders for test
Experiment 4 (2nd configuration)	They can flexibly change their route at both choice points.	Shift to left
Experiment 5 (1st configuration)	On the ground, squirrels orient to the start point, not the baited ladder.	Remove the start point ladder
Experiment 5 (2nd configuration)	Squirrels orient to the ladder closest to the start point, not the baited ladder.	Remove 2 ladders: start point and adjacent ladder

were three small clearings (Sites A, B, and C) among the redwoods, bordered by a small stream (Strawberry Creek). Different squirrels were resident at each site. For each experiment, the maze was placed in the same location and spatial orientation throughout the training period. The maze was carried to the location every day, and thus squirrels were only exposed to it during these testing hours. Data were collected from 1000 to 1600, 5 days a week, from January to November 1997. Experiments are presented in the order in which they were conducted.

Apparatus

The maze was constructed from plastic ladders (0.15×2.70 m) hanging from a steel pipe (3 m length, 1.9 cm diameter), supported by two upright steel pipes (2.7 m length, 1.9 cm diameter). The pipes were held upright in PVC pipe (4 cm diameter), embedded in two concrete-filled, white plastic buckets. The maze itself consisted of a series of plastic ladders (0.15×2.70 m) suspended from the top bar. Ladders were constructed from black plastic mesh (mesh size = 3 cm). In some experiments, some black ladders were replaced with a ladder that differed both in texture (mesh size = 4.5 cm) and color (bright orange). The top rung of the ladder was secured to the horizontal pipe, and the bottom rung was staked to the ground to provide a taut surface for climbing. A horizontal ladder of the same material and width was stretched between the two vertical pipes at a height of approximately 1.8 m. We altered the spacing between vertical ladders among experiments to enhance differences between routes; spacing was irregular in Experiments 1, 2, and 3 and regular in Experiments 4 and 5.

An aluminum weigh boat (5 cm diameter) served as a bait receptacle. One bait cup was glued to each branch ladder, 40 cm below the top bar. The target cup was baited with one unshelled raw peanut; this bait type was used throughout habituation, training, and testing phases of all experiments. The maze was only baited during habituation and training trials; squirrels were rewarded with a peanut after each test trial.

In each experiment, different routes on the maze were created either by adding or subtracting baffles or rolling up and down the ladders. Baffles consisted of two rectangular ($20 \text{ cm} \times 15 \text{ cm}$) panels, constructed either from white, foam-core board (6.3 mm thick) or clear acrylic (2 mm thick). The panels were attached on either side of the ladder with metal hinges, which allowed the baffle to be erected perpendicular to the ladder, rendering it impassable, or if it was folded down, allowing the squirrel to easily climb past it. Using probe trials during training, we found that squirrels could not distinguish, from the ground, whether a baffle was erected or folded down, and, therefore, baffles themselves could not act as cues, which allowed squirrels on the ground to see the correct route. Thus, the presence of the baffles could not have influenced their choice of routes during test trials.

Procedure

Habituation. Squirrels were familiarized with the apparatus during one initial habituation phase. During this phase, the maze was reduced to one ladder, which was placed pseudorandomly in one of the four positions. A different position was chosen daily. Each squirrel was trained individually; any other squirrels in the vicinity were given an ad lib supply of peanuts, which kept them away from the apparatus and minimized disturbance to the trainee squirrel. This method was used throughout all experiments.

Habituation was accomplished by first placing peanuts on the ground at the base of the ladder. When the squirrel reliably

approached the ladder, a series of peanuts were then placed on the fretwork of the ladder, at intervals of 15 cm. When the squirrel had consumed all the peanuts on the ladder, it was rebaited with peanuts that were placed higher up on the ladder. This process was continued until the squirrel would climb an unbaited ladder without hesitation, a process that took approximately 3 weeks for a completely naive squirrel.

Training. The goal of this phase was to train each squirrel to retrieve the bait peanut from a fixed location and to reach this location using only one route. The route was prescribed by the pattern of accessible ladders. The squirrel was allowed to explore the entire apparatus until it found a peanut, which signaled the end of that trial. Once the squirrel had consumed the peanut, it was lured off the maze, using another peanut, and the cup was rebaited. Squirrels always exited the maze by jumping off the maze from the top bar to the trunk of an adjacent tree; they never climbed down the maze, perhaps because of their natural preference to maintain a high perch during foraging. On any trial where the squirrel did not find the baited cup, it was lured to the correct cup with a peanut by the experimenter. The squirrels were initially allowed many trials per day (Experiment 1, range = 1–11), but this was later limited to five trials per day (Experiments 2–5). The experimenters moved around the maze during the procedure, feeding peanuts to other squirrels, to keep them away from the apparatus. Our test criterion was three consecutive, errorless trials.

Testing. After the squirrel reached the test criterion, it was tested with the maze in the same or different configuration but with no bait present. After each test, the squirrel was lured off the maze and given several nuts to keep it off the apparatus. The order of test conditions (e.g., unmanipulated, manipulated) was counterbalanced. Baseline trials, which were identical to training trials described above, were run between tests to bring performance back to the test criterion level. On the test day, a squirrel was tested once on each test condition (e.g., one unmanipulated test and one rotation test per day). Before each test, the squirrel was given an average of two baseline trials (with bait present), although in some cases, a squirrel suddenly climbed on the maze before it could be given a baseline trial. This was rare, however, and every effort was made to ensure that squirrels received at least one baseline trial before every test. Each squirrel was tested only once per test condition, except where noted; to reduce carryover effects, we only used the first test trial in our analyses. Test days were separated by a 2-day interval.

Data Analysis

Analyses are based on the squirrel's choice of ladder on the first trial under each maze condition. We defined a *choice* as the first ladder where all four paws were off the ground (ground choice) or off the horizontal ladder (branch choice). Routes are designated by the choice of ground (e.g., G1) or branch (e.g., B4) ladder (Figure 1). For instance, G1–B3 indicates that the squirrel chose the first ground ladder and the third branch ladder. Although other measures, such as a squirrel's latency to choice, would be potentially interesting, we could not reliably determine the start time of a squirrel's trajectory from the surrounding area to the maze.

The squirrels' choices were analyzed separately for each condition (unmanipulated or manipulated) and each choice (ground or branch) using a test of significance of a binomial proportion (Snedecor & Cochran, 1967). Specifically, we computed the probability that the sample proportion—the number of squirrels choosing the majority ladder (i.e., the ladder chosen by the greatest number of squirrels)—diverged from a normal distribution of choices. The formula for this test yielded the z value, corrected for

continuity (z_c ; Snedecor & Cochran, 1967). All tests were two-tailed, with an alpha level of .05.

Experiment 1

The goal of this experiment was to determine whether squirrels use a beacon such as the odor of the bait, or local cues, such as the appearance or odor of the correct ladder to find the baited location. First, we removed the bait itself to determine if squirrels oriented to its presence. Second, we rotated the apparatus 180° on its center axis. If squirrels orient primarily to local cues, then they should use the same ladders they used during training, even if these ladders now lead to a new location in space relative to extra-maze cues. In contrast, if squirrels used an ideothetic or allothetic frame of reference, then they should follow the same route as during training.

Method

Animals. We recruited 3 adult female and 2 adult male, fox squirrels, who were resident at Site A. One female (RER) had been tested 6 months earlier in a nonmaze memory experiment, but all squirrels were naive with regard to maze testing.

Apparatus. The ladders were arranged in two pairs, with a separation of 180 cm between the two most medial ladders. We used opaque baffles on each vertical ladder to limit access to certain ladders (Figure 1A).

Procedure. The unmanipulated trial was identical to the training procedure, except that no bait was present (Figure 1A); the purpose was to determine if the squirrels were using odor from the bait to locate the correct cup. In the rotation trial, the apparatus was rotated 180° on its center axis and every baffle was folded down, allowing the squirrel to choose a completely novel route (Figure 1B). A set of tests consisted of one unmanipulated and one rotation trial; baseline trials were run between sets.

Although each squirrel received three sets of test trials, we present the analysis for the first set only, because even for the first trial, squirrels were nearly unanimous in their choices. If testing was interrupted (e.g., by bystanders or dogs), the squirrels received an additional baseline trial, after which the testing condition was resumed, although such disturbances were rare.

Results

After habituation, squirrels required a mean of 20.6 ($SE = 2.4$) training trials to learn the maze route. In the unmanipulated test condition, all squirrels followed exactly the same route as during training (i.e., G1–B3; Figure 1A). This was a significantly nonrandom distribution of choices (ground: $z_c = 3.36, p = .0008$; branch: $z_c = 3.36, p = .0008$; Figure 1B). After rotation (Figure 1C), no squirrel used the local route, G3–B1, but instead 4 of 5 chose G1–B3, again a significantly nonrandom distribution (ground: $z_c = 3.36, p = .0008$; branch: $z_c = 2.32, p = .02$; Figure 1D). Only 1 squirrel deviated from this pattern on one choice: 1 male (Tripper) chose B1 on his first trial.

Discussion

The squirrels behaved exactly the same in the unmanipulated condition as they did during training, which indicated

that they were not orienting to the presence of the bait. Instead, the squirrels had clearly learned either the route or the location. In the manipulated condition, squirrels ignored any indication from local cues on the training ladders, which were now situated at G4–B2, but instead took the G1–B3 route. It is possible that the squirrels oriented to local cues, such as scent marks, on the ground at G1, although they could not have used the local cues to orient to B3.

Thus, it is most likely that the squirrels used either an ideothetic or an allothetic frame of reference. The ideothetic strategy seemed less likely because they often climbed the maze from both front and back and, thus, would have had to memorize two sequences of turns, each one appropriate to one side of the maze.

Experiment 2

To distinguish between the use of routes that squirrels memorized in terms of their body movements (i.e., ideothetic) and a route they learned in terms of external landmarks (i.e., allothetic), we now combined a 180° rotation with a lateral shift to the right (Figure 2C). This produced a situation where there was no ground ladder at the trained location (i.e., former G1), and there was a different ladder at the branch location (i.e., former B2). After the shift, if squirrels were using either an ideothetic strategy or an allothetic strategy that was based on intramaze cues, they would search for food at B3; if they were using an allothetic strategy that was based on extramaze cues, they would search for food at B2.

Method

Animals. The same squirrels at Site A were used, and testing occurred immediately after the completion of Experiment 1.

Procedure. We used the same training and test procedures as in Experiment 1, except that the axis of rotation was centered on B3. This resulted in a lateral shift to the right of 1.8 m. The training route was G1–B3. In the shift condition, the goal was located at B2, whereas the trained ground location was now located to the left of the maze.

Results

In the unmanipulated condition (Figure 2A), all squirrels again followed the route, which was defined by the maze during training (G1–B3; Figure 2B; ground: $z_c = 3.36, p = .0008$; branch: $z_c = 3.36, p = .0008$). After the rotation and shift (Figure 2C), 4 of 5 squirrels took G1–B2 (Figure 2D), which was, again, a significant preference (ground: $z_c = 3.36, p = .0008$; branch: $z_c = 2.32, p = .02$). One squirrel (female L–front) chose a different branch ladder (B1), which was directly above her ground choice (G1). The squirrels appeared to show no hesitation in taking the shorter route through the maze after the rotation.

Discussion

Although squirrels used the training route on the unmanipulated condition, they used a novel route after the maze was rotated and shifted. Their novel route demonstrated that they had oriented to an allothetic, extramaze frame of

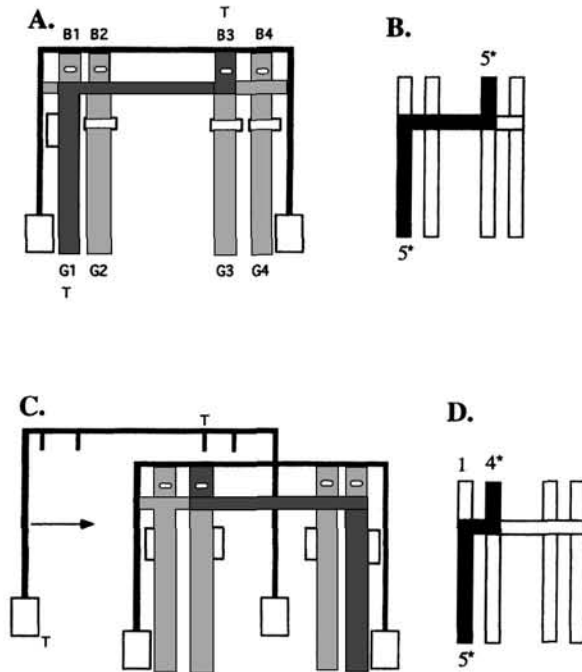


Figure 2. (A) Schematic drawing of the maze, shown during the unmanipulated test in Experiment 2; other conventions are the same as in Figure 1. (B) Results from the unmanipulated test. Solid bar = location of route relative to extramaze cues (G1–B3). The number of squirrels choosing a ladder on their first trial is shown above or below each ladder ($*p < .05$). (C) Schematic drawing of the maze after rotation and shift to the right. The arrow shows the direction of the shift. The graduations on the horizontal pole of the maze in the background indicate the original location of the ladders during training. The location of the training route relative to extramaze cues is marked with a “T” at the ground (G1) and at the end (B3). (D) Results from the rotation and right shift test. Solid bar shows the route, which is now contracted relative to extramaze cues (G1–B2; $*p < .05$). G = ground choice; B = branch choice.

reference. In contrast to Experiment 1, the squirrels could not have oriented to the odor of the ground at the training location, because this location was displaced to the left of any ladder. Instead, the squirrels chose the first ladder, G1, which was displaced 1.8 m from the training location. This suggests that during training, the squirrels were not simply orienting to an odor on the ground, although our experiment was not designed to exclude this possibility.

In light of the squirrels’ plasticity in route choice, it is surprising that once again the squirrels did not choose the shortest route to the goal (G2–B2). Perhaps the squirrels coded the location of the start point as the first ladder to the right of the aluminum pole. If so, then squirrels might have been switching between two frames of reference, using intramaze cues to determine the location of the ground ladder but using extramaze cues as the frame of reference for the branch choice. Alternately, they might have used one frame of reference but were using it to return to two locations, one on the ground and one at the branch.

Experiment 3

Another possible reason that the squirrels did not take a direct route could have been that the squirrels had difficulty visually discriminating the dark ladders from their background and perhaps did not know that all routes were accessible. Thus, we repeated Experiment 1 with new squirrels at a new site and trained them to follow a new route, which was conspicuously marked with bright orange ladders.

Method

Animals and study site. We recruited 3 adult females and 4 males at Site B. One squirrel (Female LF) had participated in Experiments 1 and 2, and another (RER) had participated in a different memory experiment a year earlier. All other squirrels were naive to behavioral testing. Site B was approximately 200 m from Site A and was also located in a small clearing, surrounded by redwoods and adjacent to Strawberry Creek on the east and a large lawn on the west. The richness of distal spatial cues appeared identical between the two sites.

Apparatus. Two sections of vertical black ladder as well as one section of horizontal ladder were replaced with orange ladders, so that the training route was completely orange (Figure 3A). New ladder sections were stapled onto the existing ladders. In addition,

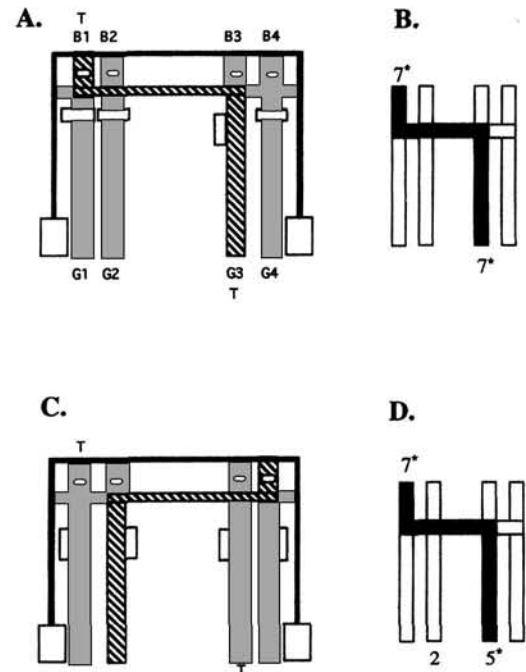


Figure 3. (A) Schematic drawing of the maze, shown during the unmanipulated test in Experiment 3. Stripes = orange training route (G3–B1). Other conventions are the same as in Figure 1. (B) Results from unmanipulated test. Solid bar = location of route relative to extramaze cues (G3–B1). The number of squirrels choosing a ladder on their first trial is shown above or below each ladder ($*p < .05$). (C) Schematic drawing of the maze after rotation. (D) Results of the rotation test, with the same conventions as before. G = ground choice; B = branch choice.

the foam-core baffles were replaced with clear acrylic baffles, to reduce the risk that squirrels would avoid ladders with visible baffles, even if they were open.

Procedure. The squirrels were trained and tested in the same manner as described previously, except that they were habituated with a single black ladder. The squirrels were not exposed to the orange ladder until the training condition commenced. The correct route was G3–B1 (Figure 3A).

Results and Discussion

In test trials, all squirrels followed the training route in the unmanipulated condition (Figure 3B; ground: $z_c = 4.15$, $p < .0001$; branch, $z_c = 4.15$, $p < .0001$). After rotation (Figure 3C), most squirrels again followed the training route. Five of 7 squirrels chose G3–B1, and both choices showed a significant departure from random distribution (ground: $z_c = 2.40$, $p = .016$; branch: $z_c = 4.15$, $p < .0001$; Figure 3D). Only 2 squirrels (female Furball and female Redflank) chose the ladder predicted by the local cue (i.e., the orange ladder that was at G2). Both of these squirrels then chose B1, which was the black ladder branch that led to the trained location place.

These results, using an altered maze, a new route, a new site, and new squirrels, replicated the results of Experiments 1 and 2. The only deviation from unanimity was the choice of a ground orange ladder by 2 squirrels, although both then subsequently chose a black branch ladder. Thus, even with more conspicuous intramaze cues and the use of transparent baffles, squirrels oriented to the location of the trained route, not the training ladder. Once again, no squirrel took the most direct route (G1–B1).

Experiment 4

Our previous results indicate that the squirrels did not use olfactory cues or other intramaze cues as beacons to locate the reward. They also did not use an ideothetic frame of reference, because they adjusted their route immediately after the shift. Therefore, they must have been using an allothetic frame of reference, which was based on extramaze cues. Their behavior, however, could not be explained by orientation to a single baited location, because they did not take a direct route when the baffles were removed. There are two explanations for this: First, they might have remembered the route in terms of two locations (the correct ground and branch choices) and were orienting correctly to two places. Second, lengthy training with baffles made it difficult for them to perceive that other routes were accessible during the test. We addressed this in Experiment 4 by training a new group of squirrels on a maze in which, instead of closing baffles during the test, we added ladders. If the baffles had influenced previous test behavior, squirrels might now use the added ladders to take the shortest route to the goal.

Method

Animals and study site. We recruited 12 squirrels: 4 adult females, 2 subadult males, and 6 adult males at Site C. One subject (female Spotted) had been tested in Experiments 1 and 2, and 2 others had been tested in Experiment 3 (female Furball, male RR).

Site C was approximately 10 m north of Site B, which was also located in a small clearing.

Apparatus. We controlled the squirrels' access to the ladders by rolling or unrolling the ladders. Rolled ladders formed a bundle, which hung 10 cm below the horizontal ladder (Figure 4A). The training ladder was made from wide orange mesh, and other ladders were made from small black mesh. During testing, all four ladders were now equidistant from each other to increase the visual differentiation between this and previous configurations.

Procedure. Only the orange ladder was available during training; the route was G2–B4 (Figure 4A). For testing, squirrels were given test sets of one unmanipulated and one rotation trial. In the unmanipulated condition, all ladders were lowered (Figure 4B), and in the rotation condition, this was combined with a 180° rotation (Figure 4D).

After all squirrels had completed unmanipulated and rotation tests, we ran all squirrels as a group in a third test, the shift condition (Figure 4F). The rightward shift in Experiment 2 produced a condition in which there was no ladder at the trained ground location (Figure 2C). In Experiment 4, we used a leftward shift so that there would be no ladder available at the trained branch location. We used the opposite direction to determine if squirrels could be flexible in their ladder use at both ground- and branch-choice points. Finally, because we suspected that the duration of training affected their flexibility of choice, squirrels were given minimal training before testing. The goal was now located to the right of the entire maze, and the training location for the ground ladder was moved from the G2 to the G3 position.

Results

After habituation, squirrels were given a mean of 9.5 ($SE = 1.5$) training trials before being tested. In the unmanipulated condition (Figure 4B), most squirrels once again followed the training route (G2–B4; ground: $z_c = 3.67$, $p = .0002$; branch: $z_c = 2.33$, $p = .02$; Figure 4C). After rotation (Figure 4D), only the ground choice showed a significantly nonrandom distribution (ground: $z_c = 2.92$, $p = .0035$; branch: $z_c = 0.73$, ns ; Figure 4E).

Because of the variability in the first rotation test trial, we decided to add a second trial in the same configuration. After two baseline trials, we were able to retest 6 of 12 squirrels; the other 6 squirrels did not return to the maze during this period and therefore could not be tested. The results from this trial were more consistent, with 5 of 6 squirrels choosing G2 ($z_c = 2.83$, $p = .0047$); 1 squirrel (female Furball) again chose G3, the orange ladder. In the branch choice, 5 of 6 squirrels chose B4 ($z_c = 2.83$, $p = .0047$); 1 squirrel (male Ali) chose B2.

After the second rotation test trial, we recruited 9 squirrels for the shift condition (Figure 4F). Seven of 9 squirrels oriented to the ladder in the training location, not to the orange ladder ($z_c = 3.27$, $p = .001$; Figure 4G). Similarly, 7 of 9 squirrels chose the branch ladder closest to the training location, which was rendered unavailable by the shift to the left ($z_c = 3.27$, $p = .001$; Figure 4G).

Discussion

Despite the change in methods, the results from Experiment 4 tallied closely with those from previous experiments. The main difference appeared in the first trial of the rotation condition. Here, squirrels consistently started at the trained

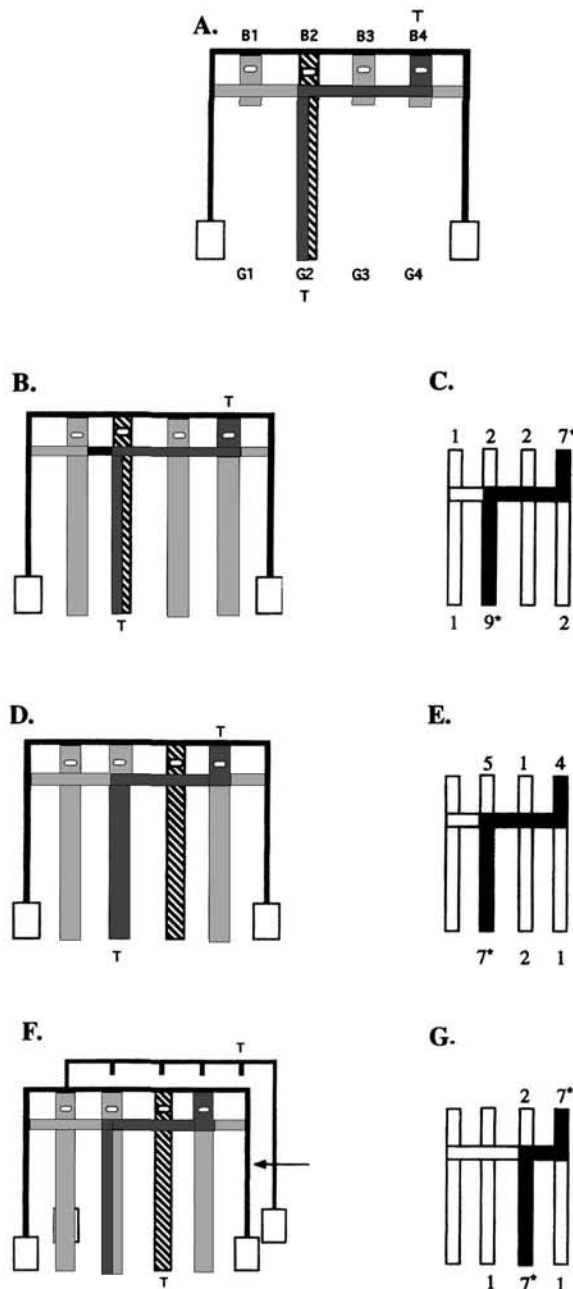


Figure 4. (A) Schematic drawing of the maze that was shown during training in Experiments 4 and 5, with only one orange ladder accessible. Striped = orange ladder; dark shading = trained route (G2–B4); G = ground choice; B = branch choice; other conventions are the same as in Figure 1. (B) Schematic drawing of the maze as shown during the unmanipulated test in Experiment 4. (C) Results from the unmanipulated test. Solid bar = location of route relative to extramaze cues (G2–B4). The number of squirrels choosing a ladder on their first trial is shown above or below each ladder (* $p < .05$). (D) Schematic drawing of the rotation test. (E) Results from the rotation test with the same conventions as before. (F) Schematic drawing of the rotation and shift test; the arrow shows the direction of the shift; the graduations represent the original locations of the four ladders during training. (G) Results from the rotation and shift test with the same conventions as earlier.

location (G2), but then half the squirrels continued up that ladder to B2. Ladder B2 was not predicted by any possible strategy (i.e., beacon, local cues, ideothetic, or allothetic; Table 1). Instead, it appeared that squirrels simply continued up the first ladder they had chosen. This had been seen in other experiments: for example, the solitary aberrant choice in Experiment 1 (G1–B1 taken, instead of G1–B3). Yet by the second trial, squirrels were again nearly unanimous in their choices. Less training (approximately half as many days) may have increased this variability in the first trial. These results also demonstrate that the squirrels' failure to use a direct route in previous experiments could not be attributed to the use of baffles during training.

The shift manipulation revealed that squirrels could use allothetic cues in their ground choice as well as in their branch choice, as illustrated in Experiment 2. The squirrels scaled the correct ground ladder and then shifted their search to B4, which was the ladder closest to the trained location. Again, this was a familiar pattern, which was seen across all experiments: The squirrels would not take the shortest route to the goal but, if forced to detour, would choose the closest ladder to the trained location. To determine if squirrels were orienting to two goals (e.g., start and end points), we continued testing the squirrels with a new manipulation: subtracting certain ladders during test trials.

Experiment 5

If squirrels organize their behavior in terms of two locations, the beginning and the end of the training route, then if deprived of reaching these locations, squirrels should choose the next closest ladder. Thus if the training ladder (G2) were unavailable, they should take the next closest ladder (G1 or G3) (Figure 5A). If G3 were unavailable, and if they were orienting to the start location, they should then take G1 (Figure 5C). Alternately, if they only oriented to one location (bait at B4), they should always take G4–B4. To test this hypothesis, we trained squirrels with one ladder and then made one or two ladders unavailable during testing by rolling them up.

Method

Animals. This experiment was conducted after the conclusion of Experiment 4. Only 8 of the 12 squirrels trained in Experiment 4 were available for the first configuration in Experiment 5, and only 4 of these squirrels were available for the second configuration. This gradual attrition appeared to be due to the squirrels spending more time harvesting and caching acorns that became available at this time, and subsequently, they were less likely to show up at our study site.

Procedure. We used the same training route and training procedure. Once squirrels were readily ascending the G2–B4 route, two configurations were used to see if they would choose the direct route when the training route was unavailable, or if they would choose the ladder adjacent to the training route. Therefore, in the first configuration, the training ladder (G2) was rolled up (see Figure 5A). We rolled up both G2 and G3 ladders in the second configuration (Figure 5B) to provide two clearly differentiated choices on the ground: a ladder leading directly to the goal or a ladder adjacent to the training location. Training trials were interposed between the first and second configurations. Squirrels

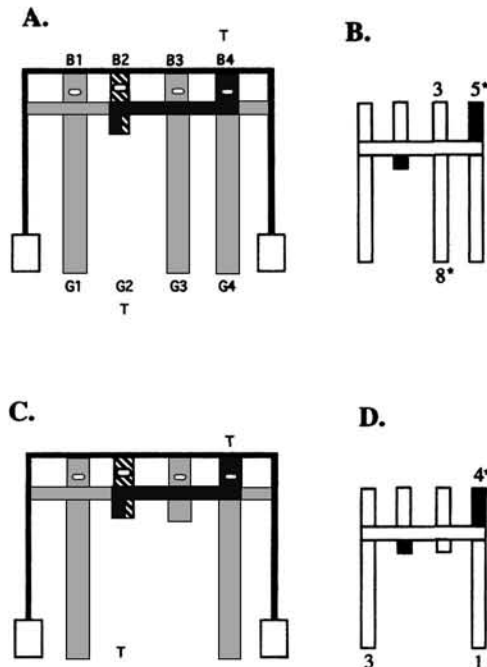


Figure 5. (A) The first maze configured for Experiment 5, after training with only one ladder, now with the training ladder (G2) rolled up. The darkly shaded ladders represent the position of the training route (G2–B4). G = ground choice; B = branch choice. (B) The results from the first test configuration. The number of squirrels choosing a ladder on their first trial is shown above or below each ladder (* $p < .05$). (C) The second configuration used for testing: The training ladder (G2) and the immediately adjacent ladder (G3) are rolled up. (D) The results from the second test configuration.

were tested on the two configurations sequentially because we reasoned that the negative consequences of carryover effects in a detour experiment like this would outweigh the benefits of controlling for order, especially because we had seen no order effects in previous experiments.

Results

In the first test, where only the training ladder (G2) was rolled up (Figure 5A), all 8 squirrels chose G3 ($z_c = 3.63$, $p = .0003$) and 5 of 8 squirrels chose B4 ($z_c = 2.04$, $p = .041$; Figure 5B). The remaining three squirrels (male RR, male LR, and male Pirate) chose B3.

In the second configuration of the maze, where both the training ladder (G2) and G3 were rolled up (Figure 5C), 3 of 4 squirrels chose G1; male L-RJ chose G4 (Figure 5D). This was not a significant departure from a random distribution ($z_c = .50$, ns). However, at the branch choice, all squirrels chose B4, which was significantly nonrandom ($z_c = 2.89$, $p = .0039$).

Discussion

This experiment addressed the following question: When a route from the correct ground location is not available, do

squirrels simply choose the shortest route to that goal? The answer was clearly no: In both configurations, squirrels were significantly more likely to choose the ladder that was adjacent to the trained ground location; the most direct route was chosen only once by 1 squirrel in the second configuration. Instead, in the first configuration, all squirrels chose the ladder to the right of the trained location. They may have chosen this ladder because it was closer to the final goal, even if it was still not the most direct route. However, in the second configuration, with both G2 and G3 unavailable, most squirrels took G1, which was the most distant ladder from the branch goal but closest to the trained ground location; this result was not significant, probably because of the small number of subjects at this point in our study. Yet, summarizing results over both configurations, we found that 11 of 12 squirrels chose an indirect route (i.e., not G4–B4). Thus, overall, this suggests that squirrels did not organize their orientation to the maze solely in terms of the location of the reward. Consistent with our earlier results, they appeared to organize their route in terms of a start and an end point.

General Discussion

The purpose of this study was to use a laboratory technique, the maze, in the field to measure the mechanisms of spatial orientation in a wild rodent. Specifically, we designed a vertical maze to measure these properties in an arboreal rodent, the fox squirrel. To return to a remembered location on the maze, a squirrel could use three possible strategies: first, an ideothetic frame of reference by coding location relative to its body position. Second, it could use an allothetic frame of reference by coding location relative to intra- or extramaze cues. Third, a squirrel could orient to olfactory or visual beacons (e.g., the peanut bait) or orient to local cues, such as a scent trail or conspicuous visual cues, on the training ladders. The results from our experiments support the conclusion that the squirrels oriented primarily to an allothetic frame of reference.

There was no evidence that the squirrels oriented preferentially to the bait as a beacon, although we did not rule out the possibility that squirrels had acquired this information but did not use it. Indeed, squirrels may well use such information under other experimental conditions—for example, if we had moved the peanut to a novel location. However, in the present study, the squirrels' behaviors were not affected by the removal of the bait, which demonstrated that they were not using it as a primary source of spatial information.

In general, squirrels also ignored local cues: When rotation of the maze dislocated local cues from their spatial location relative to extramaze cues, squirrels chose ladders that were correct in relation to extramaze cues and showed no sign of using local cues. Although in many configurations, the squirrels could have oriented to scent marks under the training ladder, this mechanism cannot completely account for the squirrels' choices after the shift manipulations. Even after we increased the saliency of the training route by changing both its color and texture (Experiments 3, 4, and 5), the squirrels continued to rely on an external frame of reference—not local cues—for orientation. The only

deviation from this pattern occurred in Experiment 3, when the training route was outlined in orange ladders: In this configuration, 2 squirrels chose the orange ladder after the rotation. Future studies that manipulate the saliency of the local cues to an even greater degree might predictably increase the use of local cue information.

Laboratory rats that solve the radial arm maze also rely on local cue information only under certain circumstances. For example, if visual cues are available, rats do not use intra-arm cues such as odor trails to solve the radial arm maze (Olton, Collison, & Werz, 1977). However, if visual cues are not available, rats can rely on olfactory cues, which suggests that these cues have been implicitly coded but are not explicitly used for orientation when distal visual landmarks are available (Lavenex & Schenk, 1995, 1996). Nonetheless, one might predict that this highly visual species might rely more heavily on visual than olfactory cues for spatial orientation than the largely nocturnal laboratory rat. Fox and gray squirrels have dichromatic color vision (G. H. Jacobs, 1974, 1976), and they use color as a cue for efficient foraging, both in the laboratory (King, Flaningam, & Rees, 1968; McQuade, Williams, & Eichenbaum, 1986) and in the field (Macdonald, 1992, 1997). Although fox squirrels, like laboratory rats, did not use color cues in an explicit manner to solve the maze, perhaps they coded color in an implicit manner and could rely on this information for orientation if other cues became unreliable.

The squirrels also did not preferentially code the location in terms of an ideothetic frame of reference. After the shift manipulations (Experiment 2 and 4), the squirrels adjusted either their ground choice or their branch choice on the first trial. Thus they immediately changed the series of body movements that they had used previously in order to reach the correct branch ladder.

This behavioral plasticity suggests that they were relying primarily on an allothetic frame of reference and that it was not based on intramaze cues. When the training ground ladder was unavailable in Experiment 2, they chose the next closest ladder. When the training branch ladder was unavailable in Experiment 4, they again chose the next closest ladder. Using an intramaze strategy, they would have continued to follow the same route in the maze, even after shift or rotation.

Thus, overall, our results are consistent with the hypothesis that squirrels rely primarily on an extramaze frame of reference. This result would be predicted from studies of another scatterhoarding species, the black-capped chickadee, which also shows a preferential orientation to the absolute location of a reward, as opposed to its location within an experimental apparatus (Brodbeck, 1994; Herz, Zanette, & Sherry, 1994). This preference also agrees with results from free-ranging animals: Rufous hummingbirds (*Selasphorus rufus*) preferentially reorient to the location, not color, of a previously rewarded flower (Hurly & Healy, 1996). Finally, we have found recently that free-ranging fox squirrels solve a memory task (remembering which cups are baited in a symmetrical array) by giving priority to distal cues (e.g., trees and logs) over proximate, intra-apparatus cues (e.g., edges of experimental board). Squirrels continued

to show this strong preference even when proximate cues were the best indicators of reward location (Lavenex et al., 1998). Thus, studies of free-ranging animals lend further support to the hypothesis that extramaze, distal cues are the preferred source of spatial information.

Although squirrels used distal cues for orientation and showed a flexible response to detours and shifts, they almost never took the shortest route to the goal. If this indicates that they had not formed a cognitive map (Tolman, 1948), then there are several possible explanations.

One explanation for their failure to choose direct routes is that they had never explored each possible route in both directions. Bidirectional exploration is necessary for laboratory rats to use novel short-cuts in the three-platform maze (Ellen, Soteris, & Wages, 1984; Maier, 1932; Thinus-Blanc, 1996). Because our squirrels did not explore the maze in two directions, they might not have integrated all possible routes into their representation of the reward location. On the other hand, the squirrels had explored the points of intersection between ladders, which is the critical component to forming a map-like representation (Thinus-Blanc, 1996). Also, in contrast to laboratory rats learning a novel maze in a novel environment, our squirrels were intimately familiar with the local scene, and it thus seems unlikely that they could not conceive of the direct route because of their inexperience.

A more likely explanation is that the squirrels had learned to solve the maze as a simple conditioned association between a certain route and a reward. Because squirrels were not rewarded during test trials, but only afterwards, it is possible that they had learned that the reward was conditional on their use of a certain route.

If they had indeed learned a route and not a single location, it is still important to know how they encoded this information. It is clear that they did not store it as an ideothetic strategy that was composed of a memorized sequence of turns, because they easily adjusted their route after a shift. Instead, they may have learned to associate a sequence of local views (or visual snapshots) with the probability of reward. In the terminology of cognitive maps, instead of using a geometric "locale" map, perhaps the squirrels had learned a route or "taxon" map (O'Keefe & Nadel, 1978). Others have suggested that such route maps, which are made up of local views, can be combined later with path-integration processes to form a comprehensive map of the environment (McNaughton, 1988; Thinus-Blanc, 1996).

Such a local view scenario could explain our results in the following manner: A squirrel would orient to the maze by matching the local view at a particular ground ladder with a template of the rewarded route that was stored in memory. Once it had matched perception and memory, it would then climb that ladder, traverse the horizontal ladder until it perceived the next matching local view, and then ascend the appropriate branch ladder. Rotation would not influence its perception of local views and, therefore, not change its behavior; a maze shift would cause the squirrel to change the horizontal distance traveled (either increasing or decreasing it) before finding the correct match.

This explanation would only be complete if the squirrels

were orienting to two local views: the view at the start point and the view at the reward. However, our results support this interpretation. Across all experiments, with 11 different maze configurations, the squirrels returned to the location of the two ladders on which they had been trained. The only exception was seen in the first trial after rotation in Experiment 4, where half the squirrels continued up their ground ladder choice to the branch above. Otherwise, squirrels returned to their trained places. When their previous route was unavailable, as in the shift manipulations of Experiments 2 and 4 or the roll-up manipulations of Experiment 5, the squirrels continued to select the ground ladder closest to their training location, not the ladder directly beneath the goal. In fact, in the configuration where just the training ladder (G2) was rolled up, all squirrels chose the ladder that was adjacent to it (G3); no squirrel chose either the direct route (G4-B4) or the adjacent ladder farthest from the branch goal (G1). Perhaps squirrels had not only learned two local views, one from the ground and one from the horizontal branch, but had also learned which elements these two views had in common (i.e., the notion of shared elements or fragment fitting, which has been suggested to be the basic building block of spatial representation in the rodent; Thinus-Blanc, 1996; Worden, 1992). If so, then they would be more likely to choose that ladder that also has those common features—this would be G3, not G1.

A hypothesis of two local views would also be consistent with studies of laboratory animals. For example, rats that are trained to solve a branched, or hierarchical, radial arm maze show errors on the primary branch that are independent of errors made on secondary branches (Roberts, 1979). Schenk has also described a two-step process used both by laboratory rats and marmosets (*Callithrix jacchus penicillata*) to solve a three-dimensional cube maze in two steps, the horizontal and the vertical components (Grobéty & Schenk, 1992; Schenk, Grobéty, Lavenex, & Lipp, 1995). Our ground and branch choices could also be seen as the squirrel's decision to locate itself at a certain vertical and horizontal displacement, where errors at the primary branch (ground choice) would be independent of errors at the second choice point (branch).

In conclusion, free-ranging fox squirrels used mechanisms of spatial orientation that are similar to those seen in other species, both wild and domestic, under laboratory conditions. Thus, mechanisms of spatial orientation may not only show striking convergence across species but can also transfer with little distortion between experimental contexts.

Yet future research may disclose important differences between behavior in the laboratory and the field. Despite the results of this study and similar results from the use of a maze to study spatial memory in free-ranging hummingbirds (Healy & Hurly, 1995), at this point, we are only beginning to explore the range of possible learned behaviors in wild birds and rodents. As we continue to study learning in the field, we may find that free-ranging animals store or use spatial information in ways that are qualitatively different from an animal confined in the laboratory. And if we are to understand the adaptive significance of learning, we must also ask: In what context is learning critical for survival?

The fundamental problems faced by foragers—the perception and discrimination of prey items, tracking the spatiotemporal distribution of food sources, and optimizing patch choice decisions—all have important cognitive components. How these are informed by learning ability in the field is an important question that is still largely unanswered (Kamil, 1994). By combining laboratory and field methods, future research may reveal more precisely what animals learn under natural conditions and how this information is used.

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