Spatial Versus Nonspatial Relational Learning in Free-Ranging Fox Squirrels (*Sciurus niger*)

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This experiment was designed to assess spatial and nonspatial relational learning in free-ranging squirrels. The authors tested the possible use of proximal landmarks as conditional information to predict the locations of nuts, hidden in small dishes distributed on a plastic board. Squirrels were trained to associate the presence of 1 object, at the center of the board, with 1 set of baited dishes, whereas the presence of a 2nd object, placed alternatively at the same location, was associated with another set of dishes. They did not acquire the nonspatial relational task on the basis of proximal landmarks. They developed a win-stay spatial strategy relying on directional information derived from distant visuospatial cues and neglected proximal spatial information when it conflicted. They relied on their memory of the food locations in the previous trial to predict the nuts' locations, even though the objects were the only predictors of these locations.

Gray squirrels (*Sciurus carolinensis*) have been shown to rely on spatial information to locate stored food, whether they looked for their own caches (L. F. Jacobs & Liman, 1991) or for artificial caches made by the experimenter (Mac Quade, Williams, & Eichenbaum, 1986). Food-storing behavior has been related to the preferential reliance on spatial information to locate caches in mammals (L. F. Jacobs 1992b; L. F. Jacobs & Liman, 1991) and birds (Balda & Kamil, 1989; Bennett, 1993; Brodbeck, 1994; Clayton & Krebs, 1994). In these studies, animals were usually shown to rely on spatial information rather than on local features of the goal to retrieve food. The nature of the spatial relational information has, however, rarely been studied (but see Bennett, 1993; Brodbeck, 1994). One aim of the present study was to assess the importance of spatial information for free-ranging squirrels to locate food sources in the field, in particular the relative weight of proximal versus distal spatial information when no local features mark the food locations.

If enhanced spatial information processing has influenced the development of cognitive traits through natural selection, it does not imply that the cognitive abilities of food-storing species are strictly limited to the processing of spatial information. Such information, that is, an allocentric spatial representation coding the relational properties or the configuration of environmental cues, constitutes a particular

case of relational or configural representations that are not necessarily limited to spatial information (Eichenbaum, Fagan, Mathews, & Cohen, 1988; Eichenbaum, Otto, & Cohen, 1994; Sutherland & Rudy, 1989). The second aim of this study was to assess the possible reliance on nonspatial relational representations to predict the locations of nuts by free-ranging fox squirrels (*Sciurus niger*).

Field studies have shown that food-storing behavior in tree squirrels is much more complex than previously thought. Squirrels process conditional information that influences their caching decisions. Gray squirrels' caching decisions are influenced by the perishability of acorns (Hadj-Chikh, Steele, & Smallwood, 1996), the infestation by parasites (Steele, Hadj-Chikh, & Hazeltine, 1996), and the handling time (L. F. Jacobs, 1992a) and germination schedules of acorns (Fox, 1982; Steele et al., 1996). Squirrels excise the embryos of acorns of white oak species that would otherwise germinate during the winter, whereas they bury acorns of red oak species without excising the embryo, as these species will not germinate before the spring. In the field, squirrels retrieve and recache the nuts they had previously buried (L. F. Jacobs, 1987). They also tend to segregate cache locations of different types of nuts (L. F. Jacobs, Shiflett, & Lavenex, 1998). Thus, the caching behavior of squirrels appears to be highly flexible, indicating that they can extract conditional information from the nuts (i.e., perishability, parasites, and germination) and respond differentially to such information. We designed a task in which two different multimodal cues could be used as conditional information to predict the locations of nuts to assess nonspatial relational learning in free-ranging fox squirrels. This task was adapted to the studied species, but the basic demands of the task were similar to those of laboratory tasks used to test nonspatial relational learning (Eichenbaum et al., 1994).

Squirrels were trained to associate two different objects to the presence of nuts in two different sets of four dishes located on a plastic board. Squirrels could predict the

locations of the nuts by associating the presence of one particular object, placed at the center of the board, with the presence of nuts in one particular set of four locations. To do this, they could not simply associate one cue with the presence or absence of the reinforcement at the location of the cue, as the two objects were placed alternatively (pseudorandom sequence) at the same location, the center of the board, distant from the locations of the nuts (not at the nuts' locations). Thus, this task was not a purely spatial task, even though it included a major spatial component: coding the locations of the nuts. Indeed, the squirrels needed to extract nonspatial relational information to solve the task: the relationship between the presence of one of two objects placed at one location and the presence of nuts in one of two sets of four separate locations. This experiment was thus designed to answer two distinct questions: first, to determine if free-ranging fox squirrels can extract conditional information from proximal landmarks to predict the locations of buried nuts; second, to determine if squirrels rely preferentially on distal or proximal spatial information to discriminate these locations.

Method

Subjects

Eight adult or subadult (>3 months old) fox squirrels (*Sciurus niger*) of both sexes (5 female and 3 male) were used as subjects. These squirrels were free-ranging animals living on the campus of the University of California, Berkeley. All of the subjects were marked with black fur dye (Nyanzol) or color-banded metal ear tags (Monel) to allow visual identification.

Apparatus

The apparatus consisted of a square board (102 × 102 cm) made of white acrylic plastic on which 25 white plastic dishes (5 cm in diameter) were arranged in a regular grid; dishes were separated by 24 cm (see Figure 1). The plastic dishes were covered with aluminum dishes (6 cm in diameter) that the squirrels had to remove to obtain a single shelled peanut. Two different conspicuous objects could be placed at the center of the board, on top of the central dish, and predicted the locations of the baited dishes (see below). The apparatus was brought to the experimental area and removed every day after testing.
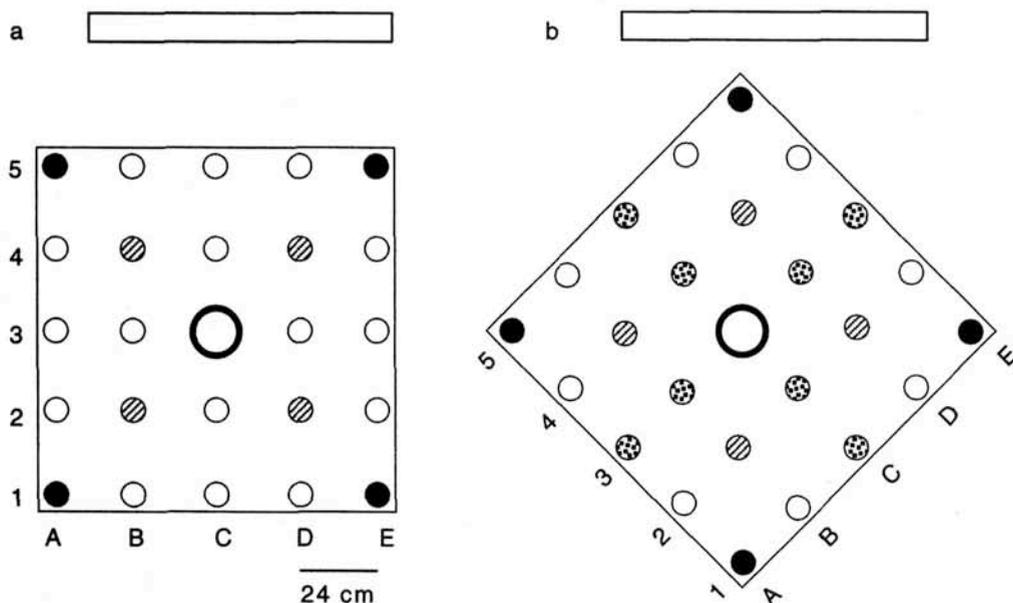
Figure 1. Schematic representation of the experimental design. The white bar (top) represents the location of a wood log located 2 m from the board, showing the orientation of the board in relation to distant visual cues from the environment (not to scale). (a) The disk at the center of the apparatus (C3) represents the location of the objects (black pipe or red cup) that predicted which array of dishes was baited. The dishes shown in black (outer array: A1, A5, E1, E5) are the four dishes baited when the black pipe was present. The dishes represented by a striped pattern (inner array: B2, B4, D2, D4) are the four dishes baited when the red cup was present. (b) Position of the board during the last three phases of the experiment after a rotation of 45° on its central axis, in relation to the position during initial training (Phase 1). Proximal dishes, represented by a solid black (outer array: A1, A5, E1, E5) and a striped pattern (inner array: B2, B4, D2, D4), were the dishes for which proximal spatial information predicted the presence of the nuts. In the first session after rotation, the black pipe was present at the center of the board, and only the dishes of the outer array (A1, A5, E1, E5) were baited. Distal dishes, represented by dots (A3, B3, C1, C2, C4, C5, D3, E3), were the dishes for which distal spatial information predicted the presence of nuts (unbaited dishes). Open circles represent "other" dishes.

Procedure

The task required the squirrels to find peanuts located in two different arrays of four locations (see Figure 1). The locations of the nuts varied between the two arrays throughout sessions. One particular object placed at the center of the board was associated with the presence of nuts in one particular array of four locations and could thus be used to predict the locations of the nuts. The first object was a black plastic pipe (30 cm high and 9 cm in diameter) and was associated with the four dishes located at the corners of the board (outer array). The second object was a red cup (12 cm high; diameter: 10 cm at the base, 6 cm at the top) and was associated with the four dishes located on the diagonals of the board (inner array). We conducted pilot experiments to confirm that fox squirrels discriminate black from red (G. E. Jacobs, 1974), and we chose different shapes to increase the discriminability of the objects.

Squirrels were trained to remove the aluminum covers on a second apparatus consisting of a single dish fixed to a piece of cardboard (25 × 25 cm). Squirrels were lured to the board with a peanut handed by the experimenter, and then were shown a piece of peanut inside the uncovered dish and were allowed to retrieve it. The peanut was then replaced, and with succeeding trials, the cover was gradually drawn across the plastic dish until it was completely covered. Squirrels were trained until they came onto the board and opened the dish within 1 min. This pretraining phase lasted for 2 to 3 days and was conducted in the same area where further testing was conducted.

The experiment was conducted in four successive phases. Each phase was aimed at answering particular questions about the use of proximal multimodal landmarks to predict the locations of food sources and about the type of spatial information (proximal or distal) squirrels use to define these locations. Squirrels were tested for no more than five trials per day throughout the experiment. Squirrels were lured to the center of the board with a peanut handed by the experimenter. They were shown the baited locations if they failed to find the nuts after 2 min on the board. The experimenter "chased" the squirrels from the board after they had found the four baited locations by presenting them with a larger piece of nut. The squirrels usually took the nut and moved away from the board to eat it. Meanwhile, the experimenter replaced the nuts at the same locations and waited until the squirrel returned to the board for the next trial. Access to the board was not restricted, and squirrels could approach from any direction. The apparatus remained stable during each daily session. It was removed each day at the end of the experimental session, but the experimenter always replaced it to the same location throughout all sessions by carefully marking the board's location on the ground. The orientation of the board remained fixed in relation to distant visual information, but one particular corner of the square board did not necessarily occupy the same location. Local cues, such as olfactory traces, were thus stable within a daily session but not between sessions. Testing was conducted during the months of June and July 1996, between 2 p.m. and 6 p.m. when squirrels were most active and most likely to come to the experimental area.

Phase 1: Initial training. During the first phase, the squirrels were trained to relate the presence of one object, at the center of the board, with one array of baited locations. When the black pipe was present, the four dishes composing the outer array were baited (see Figure 1a: Dishes A1, A5, E1, E5). When the red cup was present, the four dishes composing the inner array were baited (see Figure 1a: Dishes B2, B4, D2, D4). The order in which the two arrays were baited was varied pseudorandomly, so that the squirrels could not determine which locations were baited according to a predictable sequence throughout days. Training was conducted daily for 37

days, but as the squirrels were free-ranging animals, the number of days of testing varied among subjects ($M = 19$ days; range = 11–27 days). The sequence of testing of each subject was different, as all squirrels were not necessarily tested every day.

Four different experimental conditions were possible, depending on the baited array (outer or inner) and the array baited during the preceding session experienced by the subject (same or different): outer–different, outer–same, inner–different, and inner–same. Results were expressed as the average number of choices of the different types of dishes (correct array, incorrect array, and other dishes) for all trials in one experimental condition during Phase 1. The number of dishes of one type opened was divided by the number of dishes of this type, as different numbers of dishes belonged to the different types (correct, $n = 4$; incorrect, $n = 4$; and other, $n = 16$).

Phase 2: Rotation of the board. During the second phase of the experiment, the board was rotated 45° on its central axis in relation to its position during the first phase of the experiment (see Figure 1b). This manipulation disconnected the proximal and distal spatial information. The proximal spatial information corresponded to the spatial information as defined in relation to the board, that is, the object at the center, the edges of the board, and the rows and columns of dishes. The distal spatial information defined the space in relation to distant information external to the board, that is, trees, logs, buildings, and so on. This procedure was aimed at determining which kind of spatial information (proximal or distal) squirrels relied on to define the locations of the baited dishes. Only 7 out of the 8 squirrels previously tested were tested in this condition, as 1 squirrel disappeared from the testing area at the end of Phase 1. This second phase lasted for 8 days, and the relationship between the cues and the arrays of baited locations was maintained during the entire phase. The board remained in this position (i.e., rotated 45° in relation to the original position) for the last three phases of the experiment (Phases 2, 3, and 4).

Results were expressed as the number of choices of dishes during the first session with the board in a rotated position. Dishes are distinguished according to the different types of spatial information available (proximal, distal, or other; see below). The subsequent sessions conducted under this condition were designed to bring the squirrels back to a baseline performance between experimental manipulations and are not presented. The rotation disrupted the metric relations between the central object, the dishes, and the distant visual cues, but kept the directional information defined by the central object and distant visual cues intact. Thus, we did not distinguish between the dishes located on the inner or the outer array, even though the black pipe was present and only the dishes located at the four corners of the board were baited during the first session after rotation. The different types of dishes were defined by the directional information predicting the locations of the peanuts (see Figure 1b): proximal information ($n = 8$), distal information ($n = 8$), and other neutral dishes ($n = 8$).

Phase 3: Reversal. During the third phase of the experiment, we reversed the relationship between the two objects located at the center of the board and the two arrays of baited locations. The black pipe was then associated with the inner array, and the red cup was associated with the outer array. The location and the orientation of the board were the same as in Phase 2. This procedure was aimed at determining if squirrels had learned the relationship between the cue at the center of the board and the locations of the baited dishes. We predicted that this design would produce a decrease of performance in the first trials after the reversal of the relationship between cues and locations, if squirrels had solved the nonspatial relational task. Alternatively, squirrels should not show any change of performance after reversal if they relied on another strategy

(e.g., olfactory cues from the nuts) to solve the task. Six squirrels were tested in this third condition. This phase lasted for 4 days, and the new relationship between the cues and the arrays of locations was maintained during the entire phase. The first session in this condition (Phase 3: reversal) was conducted with the black pipe present at the center of the board with the inner array of locations baited, whereas on the last day of Phase 2, squirrels were tested with the black pipe associated with the outer array of locations. Results were expressed as the number of choices of one type of dish (correct array, incorrect array, and other dishes) during the first session in this experimental condition. Again, the following sessions were conducted to bring the subjects back to a baseline performance before the next experimental manipulation (Phase 4) and are not presented. Results were expressed as the number of dishes of one type opened divided by the total number of dishes of this type (correct, $n = 4$; incorrect, $n = 4$; and other, $n = 16$).

Phase 4: Removal of the cue. During the final phase of the experiment, we removed the center objects to determine if the squirrels were using the objects as a proximal landmark to pinpoint the locations of baited dishes. This phase lasted for 1 day, and the procedure was the same as described previously. Squirrels were tested with the outer array of locations baited without any cue at the center of the board, after they had been tested with the red cup associated with the outer array during the last session of Phase 3. The orientation of the board was the same as in Phases 2 and 3. Five squirrels were tested in this fourth condition. Results were again expressed as the number of dishes of one type opened divided by the total number of dishes of this type (correct, $n = 4$; incorrect, $n = 4$; and other, $n = 16$).

Data Analyses

The tables and figures present the number of dishes of the different types (correct, incorrect, or other for Phases 1, 3, and 4 and proximal, distal, or other for Phase 2) opened at the first dish opened (first choice) and in the first four dishes opened (first four choices). Data of Phase 1 were segregated according to the array baited (inner and outer) to demonstrate the influence of the locations of the baited dishes on the searching efficiency of squirrels. The data were also segregated according to the array baited during the preceding session experienced by the squirrels (same or different) to detect any carryover effect from the previously baited locations.

During Phase 1, the statistical analyses were conducted first on the number of correct choices with three-factor analyses of variance (ANOVAs) with repeated measures. The factors included in the analyses were (a) the array of baited dishes (inner, outer), (b) the array baited during the preceding session experienced by the

subject (same or different), and (c) the trials within a daily session (Trials 1 to 3) as repeated measures. The number of different types of choices (correct, incorrect, or other) was analyzed using a repeated measures ANOVA, an analysis commonly used in spatial learning studies to compare similar variables, such as the time spent in different zones in open-field arenas. Post hoc analyses were carried out with Fisher-PLSD tests with an alpha level of .05. The analyses of the results were conducted only on the first three daily trials, as some squirrels failed to complete five trials per day in every condition.

In Phases 2, 3, and 4, only results from the first session can unambiguously demonstrate how squirrels responded to the experimental manipulation, and hence only these results are presented. We conducted a global ANOVA with choice type (proximal, distal, or other; correct, incorrect, or other) as factors to demonstrate the differential evolution of choices throughout trials during the first session after rotation of the board. We then conducted a repeated measures ANOVA to compare the number of choices of the different dish types during each trial. No sex differences were observed, so data of both sexes were pooled for the analyses.

Results

Initial Training

Table 1 represents the number of choices of dishes of different types (correct array, incorrect array, and other dishes) for the first dish opened. This is presented as a function of the baited array, the array baited during the preceding session experienced by the squirrel, and throughout trials within a daily session. The number of correct choices was clearly influenced by the array of baited locations, $F(1, 28) = 7.14, p = .02$ (outer > inner), and the array previously baited, $F(1, 28) = 8.00, p = .009$ (same > different), but did not vary significantly between daily trials, $F(2, 56) = 3.98, p = .06$, with no interaction between any of the factors. The number of correct choices was higher when the outer array was baited than when the inner array was baited. When the baited array was the same as that baited previously, the number of correct choices was also higher than when the array was different. During the first daily trial, squirrels chose more correct dishes than incorrect or neutral dishes when the outer array was baited, $F(2, 30) = 67.93, p = .0001$ (correct > incorrect = other). In contrast, when the inner array was baited, the number of correct and incorrect choices was not different but was

Table 1
Number of Choices (M ± SE) of Different Types of Dishes (Correct, Incorrect, or Other) at the First Dish Opened, as a Function of the Baited Array, the Array Baited in the Preceding Session, and Throughout Trials Within a Daily Session During Phase 1

Preceding session	Trial	Outer			Inner		
		Correct	Incorrect	Other	Correct	Incorrect	Other
Same	Trial 1	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.75 ± 0.13	0.25 ± 0.13	0.00 ± 0.00
	Trial 2	0.98 ± 0.02	0.00 ± 0.00	0.02 ± 0.02	0.92 ± 0.05	0.06 ± 0.04	0.02 ± 0.02
	Trial 3	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.13	0.24 ± 0.13	0.05 ± 0.04
Different	Trial 1	0.78 ± 0.12	0.13 ± 0.05	0.08 ± 0.08	0.38 ± 0.13	0.51 ± 0.12	0.11 ± 0.06
	Trial 2	0.80 ± 0.12	0.11 ± 0.06	0.08 ± 0.08	0.63 ± 0.12	0.34 ± 0.12	0.03 ± 0.02
	Trial 3	0.79 ± 0.13	0.14 ± 0.07	0.08 ± 0.06	0.48 ± 0.12	0.38 ± 0.09	0.14 ± 0.07

The header spanning "Baited array" covers the "Preceding session" and "Trial" columns.

higher than that of other dishes, $F(2, 30) = 6.65, p = .005$ (correct = incorrect > other). There was no change of performance throughout daily trials for any of the choices (correct, incorrect, or other), even though performance varied slightly from one trial to the next for some types of choices.

When the data analysis was extended to the first four choices (see Table 2), the number of correct choices was not influenced by which array was baited (inner or outer) but was clearly influenced by the array previously baited (same or different). Here, the number of correct choices increased throughout trials and showed an interaction between preceding session and daily trials: baited array, $F(1, 28) = 0.22$, $p = .64$; preceding session, $F(1, 28) = 4.31, p < .05$; trials, $F(2, 56) = 32.60, p = .0001$; and Preceding Session × Trials, $F(2, 56) = 12.07, p = .0001$. There was a higher number of correct choices when the baited array was the same as during the preceding session, but only during the first two daily trials: Trial 1 and Trial 2, both $ts(30) > 2.05$, $ps < .05$ (same > different); Trial 3, $t(30) = 0.65, p = .52$. When the baited array was the same as during the preceding session, performance increased within a daily session, but only between Trials 1 and 2: correct choices, $F(2, 30) = 4.43, p = .02$ (Trial 1 < Trial 2 = Trial 3). When the array previously baited was different, the number of correct choices increased between all three trials, $F(2, 30) = 32.53$, $p = .0001$ (Trial 1 < Trial 2 < Trial 3); the number of incorrect choices decreased, $F(2, 30) = 32.06, p = .0001$ (Trial 1 > Trial 2 > Trial 3); whereas the number of other dishes chosen did not vary, $F(2, 30) = 1.94, p = .16$. The overall number of correct choices was higher than that of incorrect choices, which was higher than that of choices of other dishes, $F(2, 62) = 149.21, p = .001$ (correct > incorrect > other).

Rotation of the Board

The results of the first session with the board in a rotated position are presented in Figure 2. Squirrels were tested with the black pipe present and the outer array baited, as in the last session of Phase 1 experienced by the squirrels. Figure 2a represents the number of choices of the different types of dishes (proximal, distal, and other) at the first dish opened. There was a difference between choices, $F(2, 18) = 7.80$,

$p = .004$, and an interaction between choices and trials, $F(4, 36) = 5.54, p = .002$. During the first trial, squirrels seemed to discriminate between potentially baited dishes as defined in relation to the distal (i.e., trees, logs, etc.) or proximal (i.e., the board) spatial information from the neutral (other) dishes, even though the difference between choices failed to reach significance, $F(2, 12) = 2.17, p = .16$. There was a higher number of choices made in relation to the board during the next two trials, whereas potentially baited dishes defined in relation to distal spatial information were not chosen more often than other neutral dishes, even though the difference was only significant for Trial 2: Trial 2, $F(2, 12) = 10.33, p = .003$; Trial 3, $F(2, 12) = 2.91$, $p = .09$.

In the first four dishes opened (see Figure 2b), the number of choices of different types of dishes revealed a difference between choices, $F(2, 18) = 15.35, p = .0001$, and an interaction between choices and trials, $F(4, 36) = 22.11$, $p = .0001$. In the first trial with the board in a rotated position, there was a higher number of choices made in relation to distal spatial information, $F(2, 12) = 16.33, p = .0004$ (distal > proximal = other). In the following trials, there was a higher number of choices made in relation to the board (proximal), with no distinction of the potentially baited dishes defined in relation to distal spatial information as compared with the other dishes: both trials, $F(2, 12) > 8.92, p > .005$ (proximal > distal = other).

Reversal Learning

The results of the first session after reversal of the relationship between objects and arrays of baited dishes (Phase 3) are presented in Figure 3. Squirrels were tested with the black pipe present and the inner array baited, after having been tested with the black pipe present and the outer array baited in the preceding session (last session of Phase 2). Figure 3a represents the number of choices of the different types of dishes (correct, incorrect, and other) at the first dish opened. The squirrels did not discriminate between the different types of dishes at the first choice. There was no significant difference between choices, $F(2, 15) = 2.16$, $p = .15$, and no interaction between choices and trials, $F(4, 30) = 0.36, p = .83$.

Figure 3b represents the number of choices in the first four

Table 2

Number of Choices (M ± SE) of Different Types of Dishes (Correct, Incorrect, or Other) in the First Four Dishes Opened, as a Function of the Baited Array, the Array Baited in the Preceding Session, and Throughout Trials Within a Daily Session During Phase 1

Preceding session	Baited array Trial	Outer			Inner		
		Correct	Incorrect	Other	Correct	Incorrect	Other
Same	Trial 1	0.75 ± 0.07	0.16 ± 0.04	0.09 ± 0.05	0.80 ± 0.08	0.17 ± 0.06	0.03 ± 0.03
	Trial 2	0.79 ± 0.06	0.19 ± 0.06	0.03 ± 0.02	0.88 ± 0.05	0.09 ± 0.03	0.03 ± 0.02
	Trial 3	0.81 ± 0.07	0.15 ± 0.05	0.04 ± 0.03	0.84 ± 0.07	0.14 ± 0.07	0.02 ± 0.02
Different	Trial 1	0.56 ± 0.05	0.36 ± 0.04	0.08 ± 0.05	0.55 ± 0.08	0.34 ± 0.05	0.11 ± 0.03
	Trial 2	0.69 ± 0.07	0.23 ± 0.04	0.08 ± 0.05	0.73 ± 0.06	0.19 ± 0.04	0.08 ± 0.05
	Trial 3	0.80 ± 0.06	0.14 ± 0.04	0.06 ± 0.05	0.76 ± 0.06	0.17 ± 0.04	0.07 ± 0.03
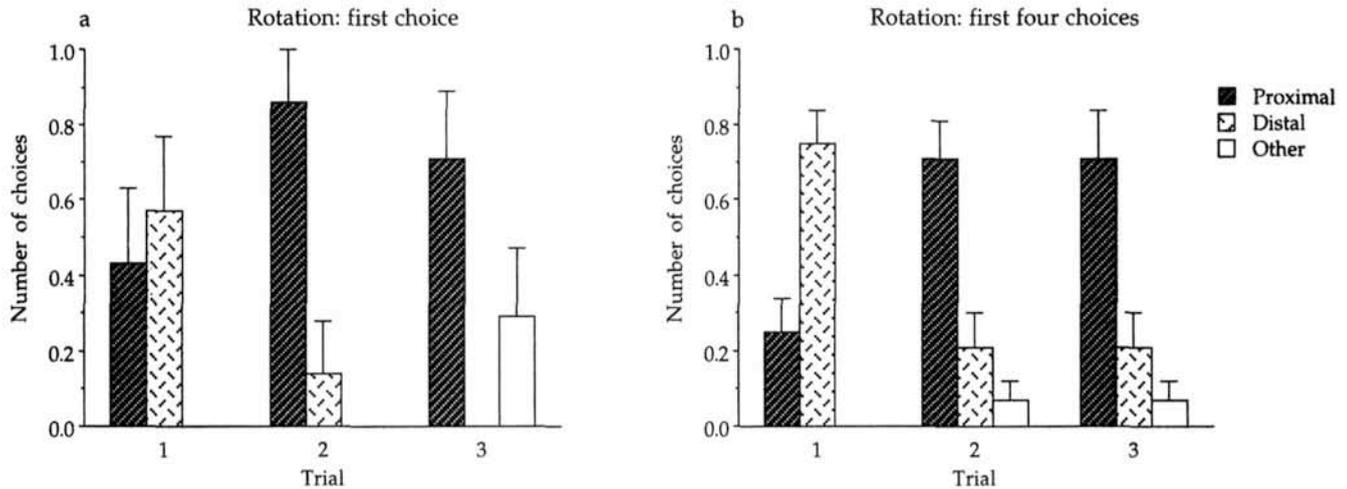
Figure 2. Performance of squirrels in the first session with the board rotated 45° in relation to its position in Phase 1. (a) Number of choices of the three types of dishes (proximal, distal, and other) at the first dish opened. (b) Number of choices of the three types of dishes in the first four choices. Proximal = correct dishes as defined in relation to the proximal spatial information (i.e., the board); Distal = correct dishes as defined in relation to distant visual cues (actually unbaited); and Other = neutral unbaited dishes as predicted by both proximal and distal spatial information (proximal or distal).

dishes opened. There was a difference between choices, $F(2, 15) = 14.34$, $p = .0003$, with an interaction between choices and trials, $F(4, 30) = 4.15$, $p = .009$. There was a higher number of correct choices for the three trials, but the difference was only significant for Trials 2 and 3: Trial 1, $F(2, 10) = 3.05$, $p = .10$; Trials 2 and 3, both $Fs(2, 10) >$

10.75, $ps < .004$ (correct > incorrect = other). Both patterns of performance (first choice and first four choices) correspond to the results obtained during the initial training (Phase 1) in the same condition independently from the cue present, that is, inner array following a session with the outer array (inner, different).
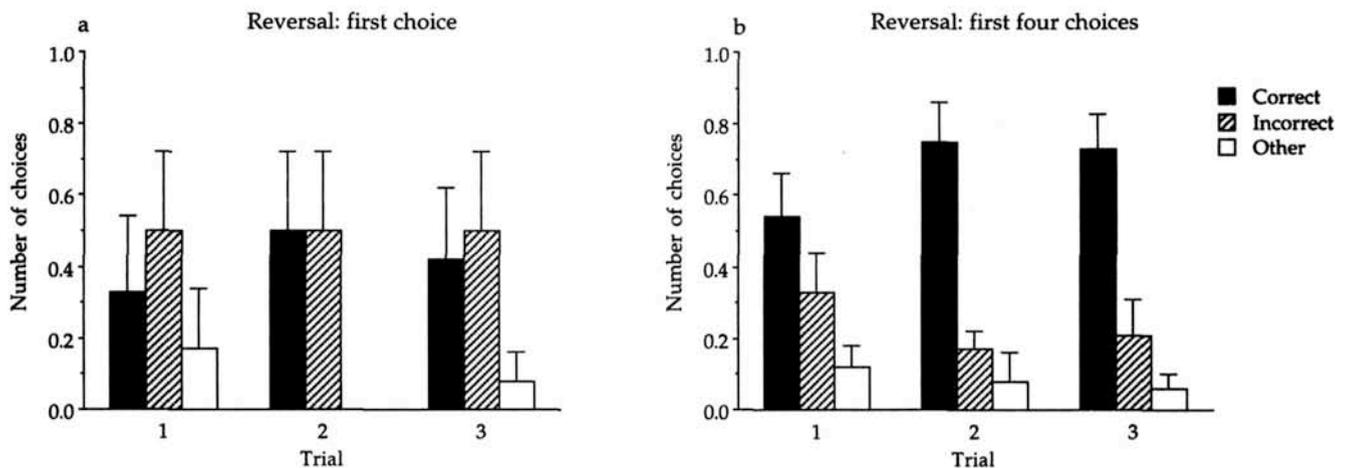
Figure 3. Performance of squirrels in the first session with reversal of the relationship between the objects at the center of the board and the two arrays of dishes. The black pipe, present at the center of the board, was associated with the inner array, whereas it was associated with the outer array during the preceding session (last session of Phase 2). (a) Number of choices of the three types of dishes at the first dish opened. (b) Number of choices of the three types of dishes in the first four choices. Correct = correct array, baited locations; Incorrect = incorrect array, unbaited locations; Other = other dishes that do not belong to one of the two arrays of potentially baited locations.

Removal of the Cues

The results of the session with removal of the cue (Phase 4) are presented in Figure 4. Squirrels were tested with the outer array of dishes baited with no cue present, after having been tested with the same outer array baited in presence of the red cup for the preceding session (last session of Phase 3). Figure 4a represents the number of choices of the different types of dishes at the first choice. There was a difference between choices, $F(2, 12) = 24.00$, $p = .0001$, without interaction between choices and trials, $F(4, 24) = 1.50$, $p = .23$. There was a higher number of correct choices than incorrect or other choices from Trial 1 to Trial 3 (correct > incorrect = other).

Figure 4b represents the number of choices in the first four choices. There was a difference between choices, $F(2, 12) = 55.70$, $p = .0001$, without interaction between choices and trials, $F(4, 24) = 0.52$, $p = .72$. There was a higher number of correct choices in the first four choices, in relation to both incorrect and other choices, from Trials 1 to 3 (correct > incorrect = other). Both patterns of performance (first choice and first four choices) correspond to the results obtained during the initial training (Phase 1) in the same condition independently from the cue present, that is, outer array following a session with the same outer array baited (outer, same).

Discussion

Free-ranging squirrels did not choose dishes by chance. The performance after reversal and after removal of the cues (Phases 3 and 4, respectively) demonstrated, however, that the squirrels did not solve the nonspatial relational task. They did not rely on the proximal multimodal cues at the center of the board to predict the locations of the nuts, even though these cues were the only predictors of these locations. Instead, they relied on directional spatial information derived from distal environmental cues (i.e., trees, logs, buildings, etc.). They relied on a spatial representation of the environment and their memory of the food locations in the preceding trial to predict the locations of the nuts.

Initial Training

Because squirrels neither chose the dishes by chance nor relied on nonspatial relational information (see below), other factors must have contributed to their foraging success. The odor of the nuts might have provided the information guiding searching behavior. Squirrels could have simply sniffed out the nuts. Yet, in the first trial after rotation of the board, the squirrels followed distal spatial information and opened dishes that had never contained a nut and that were free of any olfactory traces that might have triggered the opening of the dishes. Thus, squirrels did not rely on olfactory cues, even though we did not control for their possible use.

A detailed analysis of the choices during Phase 1 also indicates that the performance was influenced by the array baited during the preceding session experienced by the animal (same or different). Squirrels remembered the locations of the nuts during the preceding session and tended to look for the nuts where they found them previously. This tendency was particularly evident for the first trial of a day but was still visible and influenced choices during the subsequent daily trials, even after squirrels had found the new baited locations in the first trial of the day. These results demonstrate the importance of spatial information in the searching behavior of squirrels and suggest the predominance of long-term memory of food locations over more
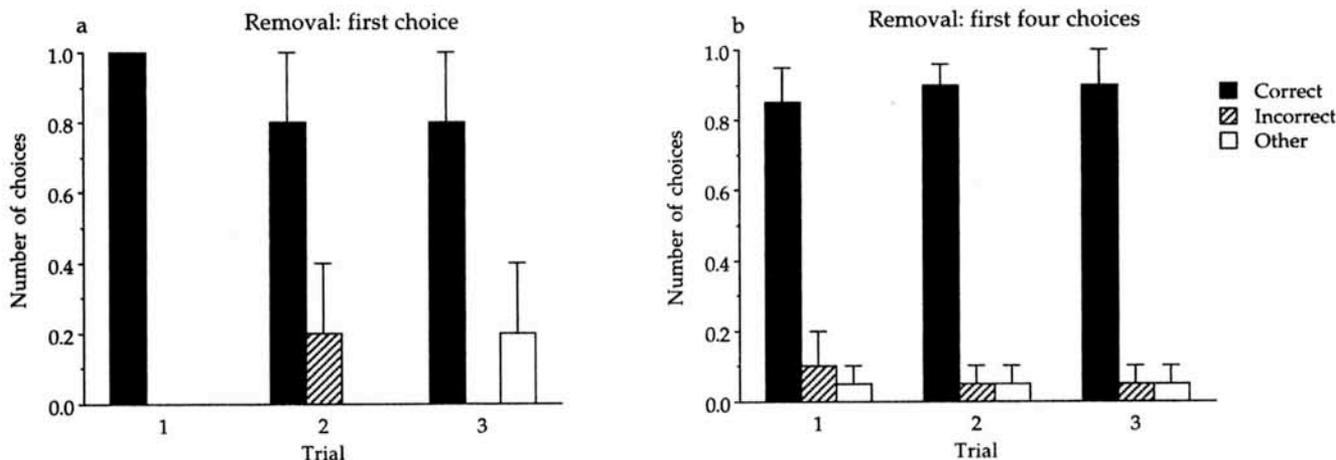

Figure 4. Performance of squirrels in the first session without any cue at the center of the board. The outer array was baited, as in the preceding session (last session of Phase 3). (a) Number of choices of the three types of dishes at the first dish opened. (b) Number of choices of the three types of dishes in the first four choices. Correct = correct array, baited locations; Incorrect = incorrect array, unbaited locations; Other = other dishes that do not belong to one of the two arrays of potentially baited locations.

recent memories or over perceptual information, such as nut odor.

Performance at the first dish opened also depended on which array was baited, which suggests that squirrels did not learn the inner array. When the nuts were located on the inner array, squirrels were still likely to first open a dish on the outer array. This behavior can be explained by the fact that squirrels encountered first the dishes located on the outer array while approaching the board, even when heading to baited dishes on the inner array, and that they checked potentially baited locations en route. The first four dishes opened showed that there was no difference in performance whether the inner or outer array was baited and showed clearly that the animals did learn both arrays.

Squirrels might also have sampled one dish located on one of the two arrays to determine which array was baited. If the first dish opened contained a nut, the squirrel could have extrapolated to the other dishes of this array and avoided opening dishes located on the other array. Because the dishes on the outer array were more likely to be opened first, the number of correct choices in the first four choices should have been higher when the outer array was baited. Yet this did not occur, and performance in the first four choices was similar for both arrays, indicating that squirrels learned both arrays similarly and did not extrapolate which array was reinforced after sampling one dish located on one of the two arrays.

Reversal and Removal

The reversal of the relationship between the cues and the baited locations did not produce any transitory decrease of performance and showed that squirrels did not rely on the cues to predict the locations of the nuts. Instead, squirrels performed exactly as in Phase 1 when tested in the same conditions, independently from the cue present (Table 1: inner–different, that is, the inner array baited following a session with the outer array baited). There was no change of performance that would have revealed the formation of a new nonspatial relational representation between the cues and the arrays. It is thus clear that squirrels did not solve the nonspatial relational task on the basis of the relations between the objects and locations.

The removal procedure confirmed that the objects were not used to predict the locations of the baited dishes and demonstrated also that they were not used as a proximal landmark to pinpoint these locations. Removal did not affect performance probably because the dishes provided salient local cues about potential nut locations, which, moreover, were primarily determined by distal spatial information. The fact that the two objects were constantly changed throughout the experiment might also explain why they were not used by the squirrels. Instead, squirrels solved the task by relying on a spatial strategy and extracted stable features of the environment to form an allocentric spatial representation (Biegler & Morris, 1993; Nadel, 1995; Poucet, 1993). Unstable, moving objects were thus unlikely to be integrated in such a representation even though they were always at the same locations, when present.

Nature of the Spatial Information

The spatial information used by squirrels consisted of directional information provided by distant visual cues. When distal visuospatial information was dissociated from proximal spatial information and local olfactory cues (nut odor), squirrels relied primarily on directional information derived from distant cues to determine the locations of the nuts, even though the exact locations were modified. In the first trial after rotation, distal information (i.e., trees, logs, buildings, etc.) predominated over proximal spatial information (i.e., the edges of the board or the rows and columns of dishes). The subsequent trials showed that squirrels quickly shifted their search to the baited locations. They might have then relied on proximal spatial information to define these locations, but it seems more likely that they learned the new locations as defined in relation to distal spatial information. These results agree with those obtained with ground squirrels (Devenport & Devenport, 1994) and black-capped chickadees (Brodbeck, 1994; Herz, Zanette, & Sherry, 1994), showing the importance of distal spatial information to determine food locations.

Our experiment differs, however, from most of the studies conducted with food-storing animals, in that it did not have local cues marking the location of the goal (or being the goal itself), which could be dissociated from distal visuospatial information ("global cues"; e.g., Clayton & Krebs, 1994). In the present experiment, only proximal and distal spatial information could be dissociated. In a laboratory experiment, Brodbeck (1994) showed that chickadees relied primarily on distal visuospatial information (in relation to the experimental room), then on proximal spatial (within the array of feeders), and finally on local visual cues (characterizing each feeder). Similarly, Bennett (1993) showed that European jays primarily remembered the position of a goal using nearby landmarks (15–30 cm from the goal and 20 cm high) and that birds obtained a sense of direction both from the landmark array and "something external" to the array. Our study demonstrates that free-ranging squirrels relied on directional information (bearings) derived from distant cues in a natural environment, whereas the influence of proximal spatial information (i.e., the board) was not unequivocally revealed in these outdoor testing conditions (see earlier). It is surprising that proximal spatial information did not influence the squirrels' choices more heavily in the first trial after rotation. However, the disappearance of the board at the end of each daily session might have reduced the salience of proximal spatial information. Yet, the corners and the edges of a white plastic board placed on a litter-covered ground provided a salient source of information; indeed, the squirrels were even hesitant to walk on the board at first.

After rotation, squirrels relied on the most reliable source of information and looked at the locations defined by the directional information derived from distant cues. They did not discriminate between dishes located on the outer or inner array as in Phase 1, probably because the metric relations between dishes and distant environmental cues had been altered. One might have expected then that the topological relations would influence choices. Indeed, topological rela-

tions have been shown to be of higher importance than metric information (Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Thinus-Blanc et al., 1987). This was not the case, however, perhaps because the locations of the dishes were now intermediate and the dishes provided a strong stimulus that attracted their attention and focused their search.

Importance of Spatial Information in a Natural Context

This experiment showed that free-ranging squirrels rely preferentially on a spatial representation to predict the locations of nuts. It does not demonstrate that squirrels are unable to form nonspatial relational representations but demonstrates that spatial information is preferentially used to guide searching behavior. It might seem surprising that squirrels did not rely on the objects (the black pipe and the red cup) to predict nut locations, as they were the only pertinent information allowing maximal performance. It is important, however, to consider that the squirrels were tested in their natural environment. They were free to come to the apparatus to perform the task or to leave the experimental area, without any form of punishment to shape their behavior. In contrast, in typical laboratory experiments, animals are confined to the experimental apparatus, and pretraining to teach which cues are relevant is usually necessary before actual tests begin (e.g., Eichenbaum et al., 1988; Staubli, Le, & Lynch, 1995). Nonnaturalistic tasks, which require long pretraining procedures, may be thus unlikely to tell us about the cognitive processes that are sensitive to natural selective pressures and that may be responsible for the evolution of a particular cognitive trait. In our experiment, squirrels were not taught what cues were relevant or any rule about the task, except that they needed to remove the aluminum cover. Under these conditions, squirrels extracted the information that was most relevant to guide their behavior in their own environment. They relied primarily on spatial information and their memory of the nuts' previous locations, which enabled them to make correct predictions in up to 80% of the cases (i.e., the last four trials of the five daily trials).

In summary, free-ranging squirrels did not acquire a nonspatial relational task on the basis of proximal multimodal cues. They extracted the relationship between distal surrounding objects to form a spatial representation of their environment. They relied on this representation and their memory of the food locations in the preceding trial to predict nut locations. This experiment demonstrates the potential of testing the cognitive abilities of free-ranging animals and the nature of spatial representations in particular. Experiments on learning and memory of nondeprived animals in their natural environment offer a unique opportunity to study the cognitive processes that are sensitive to natural selective pressures and that might be responsible for the evolution of particular cognitive traits.

References

Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. Animal Behavior, 38, 761–769.

Bennett, A. T. D. (1993). Spatial memory in a food storing corvid: I. Near tall landmarks are primarily used. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology, 173, 193–207.

Biegler, R., & Morris R. G. M. (1993). Landmark stability is a prerequisite for spatial but not discrimination learning. Nature, 361, 631–633.

Brodbeck, D. R. (1994). Memory for spatial and local cues: A comparison of a storing and a nonstoring species. Animal Learning and Behavior, 22, 119–133.

Clayton, N. S., & Krebs, J. R. (1994). Memory for spatial and object-specific cues in food-storing and nonstoring birds. Journal of Comparative Psychology, 174, 371–379.

Devenport, J. A., & Devenport, L. D. (1994). Spatial navigation in natural habitats by ground-dwelling sciurids. Animal Behavior, 47, 727–729.

Eichenbaum, H., Fagan, A., Mathews, P., & Cohen, N. (1988). Hippocampal system dysfunction and odor discrimination learning in rats: Impairment or facilitation depending on representational demand. Behavioral Neuroscience, 102, 331–339.

Eichenbaum, H., Otto, T., & Cohen, N. J. (1994). Two functional components of the hippocampal memory system. Behavioral and Brain Sciences, 17, 449–518.

Fox, J. E. (1982). Adaptation of gray squirrel behavior for autumn germination by white oak acorns. Evolution, 36, 800–809.

Hadj-Chikh, L. Z., Steele, M. A., & Smallwood, P. D. (1996). Caching decisions by gray squirrels: A test of the handling time and the perishability hypotheses. Animal Behavior, 52, 941–948.

Herz, R. S., Zanette, L., & Sherry, D. F. (1994). Spatial cues for cache retrieval by black-capped chickadees. Animal Behavior, 48, 343–351.

Jacobs, G. E. (1974). Scotopic and photopic visual capacities of an arboreal squirrel (Sciurus niger). Brain Behavior and Evolution, 10, 307–321.

Jacobs, L. F. (1987). Food-storing decisions in the gray squirrel (Sciurus carolinensis). Unpublished doctoral dissertation, Princeton University, Princeton, New Jersey.

Jacobs, L. F. (1992a). The effect of handling time on the decision to cache by grey squirrels. Animal Behaviour, 43, 522–524.

Jacobs, L. F. (1992b). Memory for cache locations in Merriam kangaroo rats. Animal Behaviour, 43, 585–593.

Jacobs, L. F., & Liman, E. R. (1991). Grey squirrels remember the locations of buried nuts. Animal Behaviour, 41, 103–110.

Jacobs, L. F., Shiflett, M. S., & Lavenex, P. (1998). The spatial categorization of scatter hoards by the fox squirrel. Manuscript in preparation.

Mac Quade, D. B., Williams, E. H., & Eichenbaum, H. (1986). Cues used for localizing food by the gray squirrel (Sciurus carolinensis). Ethology, 72, 22–30.

Nadel, L. (1995). The psychobiology of spatial behavior: The hippocampal formation and spatial mapping. In E. Alleva, A. Fasolo, H.-P. Lipp, L. Nadel, & L. Ricceri (Eds.), Behavioural brain research in naturalistic and semi-naturalistic settings (pp. 245–258). Dordrecht, The Netherlands: Kluwer Academic.

Poucet, B. (1993). Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. Psychological Review, 100, 163–182.

Poucet, B., Chapuis, N., Durup, M., & Thinus-Blanc, C. (1986). A study of exploratory behavior as an index of spatial knowledge in hamsters. Animal Behavior, 14, 93–100.

Staubli, U., Le, T.-T., & Lynch, G. (1995). Variants of olfactory

memory and their dependencies on the hippocampal formation. *Journal of Neuroscience, 15,* 1162–1171.

Steele, M. A., Hadj-Chikh, L. Z., & Hazeltine, J. (1996). Caching and feeding decisions by *Sciurus carolinensis:* Responses to weevil-infested acorns. *Journal of Mammalogy, 77,* 305–314.

Sutherland, R. W., & Rudy, J. W. (1989). Configural association theory: The role of the hippocampal formation in learning, memory and amnesia. *Psychobiology, 17,* 129–144.

Thinus-Blanc, C., Chaix, K., Bouzouba, L., Chapuis, N., Durup, M., & Poucet, B. (1987). A study of spatial parameters encoded during exploration in hamsters. *Journal of Experimental Psychology, 13,* 418–427.