

## Rufous Hummingbirds' (*Selasphorus rufus*) Memory for Flowers: Patterns or Actual Spatial Locations?

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Two field experiments were performed to examine the use of absolute and relative spatial cues by foraging rufous hummingbirds (*Selasphorus rufus*). Presented with 5 flowers arranged in a cross, birds learned that only the center flower was rewarded. When the array was shifted, birds returned to the relative center of the array when flowers were closely spaced but to the absolute location of the reward when spacing was greater than 40 cm. In Experiment 2, a 16-flower array was used, spaced either at 10 or 80 cm. Flowers were either visually identical or different, and 8 were rewarded with sucrose. Birds learned the rewarded locations more quickly when flowers were visually different. When the arrays of flowers were moved, performance was independent of flower visual patterns. At 10-cm spacing, birds tended to use relative location to recall rewarded flowers but used absolute location at 80-cm spacing.

Most animals forage on depleting but eventually renewable food supplies. Both depletion and renewal rates vary on spatial and temporal scales. For some nectarivores, such as hummingbirds, these components are typically small (several m<sup>2</sup>) and short (i.e., several hours; Armstrong, Gass, & Sutherland, 1987). When such nectarivores are also territorial, for example, the rufous hummingbird (*Selasphorus rufus*) on its breeding grounds in the Canadian Rockies, they may benefit from remembering the locations of emptied flowers. These birds could then avoid revisiting these flowers until a reasonable amount of nectar has been replenished.

The rationale for proposing such a memory ability is not simply one of calculating energetic costs of flight for a bird that investigates flowers at random. It would seem sensible also to note the vigorous enthusiasm with which these birds defend their breeding territories. A male hummingbird spends most of its day surveying its territorial borders from the top of a tall tree. Rapid detection is followed by aggressive chases of intruders, hummingbird or otherwise. Between scanning for female hummingbirds and rival birds, the male drinks from flowers or hawks insects. These

foraging bouts are brief (less than 1 min) and end with the bird returning to his sentinel post. It seems likely that these birds would take advantage of any method for reducing variation in foraging success. A rufous hummingbird that could remember both flower locations and approximate time flowers were emptied would seem to be at an advantage over more forgetful conspecifics.

The question is, can territorial male hummingbirds remember flower locations, and, if yes, how do they do so? It has now been conclusively demonstrated, by using artificial feeders both in the laboratory (e.g., Brown & Gass, 1993; Sutherland & Gass, 1995) and in the field (e.g., Healy & Hurly, 1995; Hurly, 1996), that rufous hummingbirds are able to remember locations where previously they have found sucrose. The cues they may use for accurate return to, or avoidance of, flowers have been investigated to some degree (e.g., Hurly & Healy, 1996; Miller, Tamm, Sutherland & Gass, 1985), and although hummingbirds are capable of remembering and using color and pattern features of flowers, they have a preference for returning to flowers in the appropriate spatial location. This preference for location cues over local visual cues seems sensible for a bird foraging on many flowers of the same species where the variation in the flowers' visual characteristics is far less than the variation in their spatial distribution.

There are at least two possibilities for how a hummingbird might recall a flower's location: (a) The hummingbird remembers a spatial pattern of flowers and it might recall its pattern of movement within this patch of flowers (e.g., Brown & Gass, 1993; Sutherland & Gass, 1995). Such a technique would not require a precise pinpoint memory of flower locations but perhaps memory for a clump of flowers or inflorescences (Wolf & Hainsworth, 1991). (b) Alternatively, it is possible that the hummingbird can remember individual flower locations, including locations of flowers borne by the same plant. Of these two alternatives, the latter would seem far less likely, particularly as rufous hummingbird territories contain no fewer than 200 flowers (Armstrong et al., 1987; Paton & Carpenter, 1984). In addition,

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experiments on spatial pattern learning by Sutherland and Gass showed poorer performance on complex arrays of potential food sites than on coarse-grained arrays. In these laboratory tests, birds were presented with an array of 64 visually identical feeders (purple syringe tips), 11 cm center to center, with four different patterns of feeder quality (half of the feeders contained sucrose and the other half contained water). Patterns could be as simple as assigning reward flowers to the left half of the grid or as complex as assigning reward flowers randomly. A hummingbird's memory was tested by allowing it to learn which flowers were rewarded and then switching the pattern to its mirror image. Hummingbirds took longer to relearn the random pattern than the simpler patterns. Sutherland and Gass concluded that this was inconsistent with the birds being able to remember point locations and that foragers such as these rufous hummingbirds probably develop spatially structured expectations about the quality of their environment. This spatial structuring may be akin to the chunking by food type, which has been shown to facilitate spatial memory in rats (e.g., Dallal & Meck, 1990; Macuda & Roberts, 1995).

We were interested for two reasons in exploring further the ability of rufous hummingbirds to remember flower locations in the field. First, Sutherland and Gass (1995) demonstrated that hummingbirds were able to remember the relative positions of sucrose-containing feeders in the random pattern, but it was not clear to us what the benefits are in the field of learning relative positions of flowers over memory for their actual spatial locations. Second, we wanted to investigate how unique floral cues might affect a hummingbird's ability to learn and recall a flower's location.

Previously, we have shown that rufous hummingbirds can remember up to eight different flower locations when the flowers were separated by 40–80 cm (Healy & Hurly, 1995; Hurly, 1996; Hurly & Healy, 1996). In the two experiments described in this article, we attempted to gain a clearer idea of how rufous hummingbirds remember locations of single, rewarded flowers and of multiple, rewarded flowers, both offered in an array. In the first experiment, 1 of 5 flowers was rewarded, and the 5 flowers were presented with varying distances separating each flower. In the second experiment, 8 of 16 flowers were rewarded, and both distance and color and pattern features of the flowers were varied. After reaching an acquisition criterion level, a test trial occurred in which the array was shifted relative to its original position, and the hummingbird's ability to relocate the original, sucrose-containing flowers was recorded. We made three predictions: (a) Shifting arrays of flowers would have a greater effect on a hummingbird's performance the greater the spacing between the flowers, because the relative importance of intra-array cues (for recalling relative position) and extra-array cues (for recalling spatial location) would change; (b) shifting arrays would have less effect on a bird's performance if the flowers were visually similar flowers, as the birds would have been forced to rely more on pattern or local visual cues than on location; and (c) the speed of learning initially what flowers in the array contained sucrose would be affected by the visual characteristics and the spacing between flowers. The further apart and the

more dissimilar flowers were, the easier the locations and pattern would be to acquire.

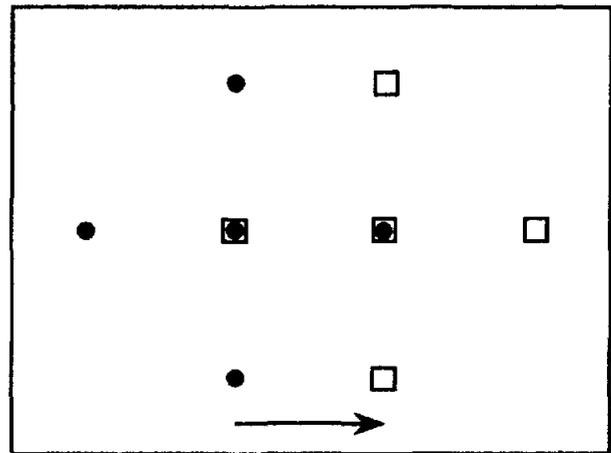
## Experiment 1

### Method

**Subjects.** The experiment was conducted along the length of a valley (1,400-m elevation) in the eastern Rocky Mountains, 20-km southwest of Beaver Mines, Alberta, Canada, (49° 29' N; 114° 25' W). Seven experimentally naïve, male rufous hummingbirds (*Selasphorus rufus*) were made individually identifiable by the application of a small amount of colored ink on their chests. Trials were run between 8:00 a.m. and 7:30 p.m. mountain standard time from May–July 1993.

**Initial training.** Seven subjects were trained to feed from small artificial flowers. These flowers consisted of a cork glued to the top of an 80-cm stake. Inserted vertically into the top of the cork was a syringe cover capable of containing 600  $\mu$ l of sucrose solution. Both the cork and the syringe tip were painted red, orange, or yellow, but each subject experienced only a single color. Hummingbirds could not empty such a flower during a single visit. Following this training to the artificial flowers, birds were presented with five flowers arranged in the pattern of a cross with 5 cm between each flower (see Figure 1). Each of the flowers in the array contained 600  $\mu$ l of 20% sucrose solution. When a bird had visited all the flowers at least twice, the outer flowers were drained, and only the center flower was refilled with sucrose solution. After a bird had fed from the center flower four times, the training trials began.

**Experimental protocol.** A training trial began with the four outer flowers filled with water (distasteful but not harmful to the birds), and the center flower was filled with 600  $\mu$ l of 20% sucrose



**Figure 1.** Experimental array of flowers for Experiment 1. Solid circles represent the array during training trials in which only the center flower was rewarded, and all others contained water. For convenience, flowers were identified as N (north), E (east), S (south), W (west), and C (center), although the array was not necessarily oriented according to the magnetic compass. Spacing between flowers was 5, 10, 20, 40, 80, 160, or 320 cm in the horizontal plane. Open squares represent the locations of flowers during a test trial in which the array was shifted one spacing unit to the E. All flowers were empty during test trials. Note that the central square is now in the location of a previously unrewarded flower, and the W square lies in the original location of the reward.

solution. A bird was deemed to have visited a flower when it probed the flower with its tongue and visited an array when at least one flower was probed. We determined that the bird had learned that only the center flower contained reward when its first flower choice on seven consecutive visits to the array was to the center flower. Once this criterion level was reached, all of the flowers were emptied and the array was shifted in one of the major compass directions (north, south, east, or west) such that the center flower now occupied the site of one of the corner flowers (see Figure 1). The order of visits to flowers by hummingbirds was then recorded. Following this test trial, the next training trial began. To do this, the array was moved to a new location at least 5-m distant, the center flower was filled with sucrose, and the outer flowers again were filled with water. Once the bird had visited the array 4–8 times (randomly determined), the array was shifted in a different direction for another test trial. This training and test procedure was repeated until the bird had been tested with shifts in all four compass directions. Birds transferred easily to the center flower when a training array of a specific size was moved to a new location; thus, training to criterion was not required.

This entire procedure was repeated by using crosses with 5, 10, 20, 40, 80, 160, or 320 cm between flowers. Each time the spacing was altered, we required the subject to achieve the criterion of seven visits to the center flower before the first test trial occurred. The order of spacing and the order of direction shifts were randomized for each subject. In each trial, the array was oriented only crudely toward the north such that precise compass information across trials was not likely useful to the subjects. Thus, compass direction was identified primarily for the purpose of eliminating directional bias during test-trial shifts.

Subjects experienced a mean of  $4.0 \pm 0.2$  test trials each day, thus requiring 6–8 days to complete all test trials. Intertrial intervals (ITIs) for training trials averaged  $12.4 \pm 0.8$  min. During ITIs, subjects engaged in natural behaviors: hawking insects, perching and vigilance, chasing of rival birds and female hummingbirds, and so forth. Arrays were placed in open areas well within a subject's territory and could be approached by the subject from any direction. Subjects usually approached the arrays directly from tree perch (2–10-m high). The open areas consisted of mosaics of short vegetation with occasional shrubs, bare patches, logs, stumps, rocks, and so forth. We attempted to ignore such objects when establishing training arrays, with the restriction that a test shift could occur without distorting the array.

All statistics we used were two-tailed probability distributions except where specified. The criterion for statistical significance in all tests was  $p < .05$ .

## Results

The performance of the subjects during the test trials supported our predictions (Figure 2). During probes, the tendency for a subject to visit the central flower varied according to the spacing of the array,  $F(6, 36) = 35.38, p < .001$ . This variation was systematic in that subjects' preference for the central flower decreased as array spacing increased (Page's  $L$  test for ordered alternatives;  $L = 906, p < .01$ ; Sokal & Rohlf, 1981). As array spacing increased, preference shifted to the actual spatial location of the reward (see Figure 2),  $F(6, 36) = 6.10, p < .001; L = 889, p < .01$ .

These data suggest that the way in which hummingbirds remember the location of a rewarding flower changes as the spacing between flowers changes, specifically, relative position for small spatial scales and absolute location for large.

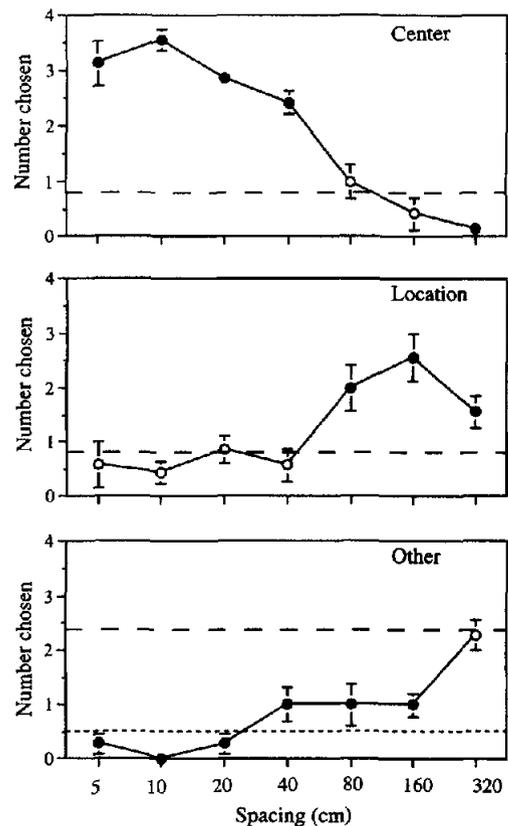


Figure 2. Mean ( $\pm$  SE) number of first choices out of four of center, location, and other flowers during test trials. Means averaged across 7 subjects. Dashed lines represent random performance ( $\frac{1}{5} \times 4$  test trials = 0.8 for location and center;  $\frac{3}{5} \times 4$  test trials = 2.4 for other). Dotted line represents background sampling rate estimated from last 20 training trials for each distance for each individual ( $12.8\% \times 4$  test trials = 0.51). Solid circles are significantly different from dashed lines, and open circles are not different (two-tailed, one-sample  $t$  tests,  $n = 7, ps < .05$ ). In addition, in the bottom panel, solid circles do not differ from the dotted line, but open circles do.

To assess the validity of this conclusion, we examined actual performance relative to chance performance. If a subject selected a flower at random, we expected the hummingbird to make a first visit to the center flower (center) one fifth of the time or 0.8 visits out of four test trials. The same chance expectation was applied to the flower in the correct spatial location (location). Visits to center were significantly above chance level for the spacings 5–40 cm and significantly below this level at 320 cm (see Figure 2; one-sample  $t$  tests,  $n = 7, ps < .05$ ). Test visits to location did not differ significantly from random until the spacing was 80 cm or greater (Figure 2; one-sample  $t$  tests,  $n = 7, ps < .05$ ). Thus, preference during probes shifted from relative position to actual spatial location as the spacing of the array increased.

During test trials, subjects sometimes made a first visit to a flower that was neither center nor location, and we classified these as other. Choice of other increased significantly with spacing (Figure 2),  $F(6, 36) = 8.46, p < .001$ ;

$L = 897$ ,  $p < .01$ . Because there were always three flowers that could be classified as other, chance performance was three fifths of four probes, or 2.4 visits. Choice of other was significantly below chance performance for all but the highest spacing (Figure 2; one-sample  $t$  tests,  $n = 7$ ,  $p_s < .05$ ).

If choices of other were not due to chance, were they due to errors? That is, did the subjects attempt to find center or location but fly to other by mistake? If other was chosen by mistake when attempting to find location, then there should be a bias toward other flowers that were closer to location. Two other flowers were 1.4 spacing units from location, and the third flower was 2.0 spacing units from location (Figure 1). The mistake hypothesis predicted that more than two thirds of the other flowers should be close to location, whereas random choice among the other flowers predicted precisely two thirds should be close to location. Of the 40 visits to other, mean performance across birds did not differ significantly from the expected value of 0.667 ( $M = 0.743 \pm 0.053$ , one-sample  $t$  test,  $t = 1.443$ ,  $n = 7$ ,  $p = .20$ ).

An alternative explanation for choices of other is that they represent sampling behavior. We know that subjects learned that the central flower was rewarded during training trials, but we did not expect them to understand that only one flower was ever rewarded. That is, they occasionally sampled noncentral flowers to determine whether they contain rewards. Choices of other may simply be sampling behavior that occurs during a test trial. To test this hypothesis, we determined the background level of sampling by counting the number of visits to the noncenter flowers during the last 20 training trials of each individual for each spacing. Overall sampling rate during these 980 trials averaged  $12.8\% \pm 1.0\%$  across subjects. Visits to other during test trials differed significantly from this sampling rate only when the spacing was 320 cm (Figure 2; one-sample  $t$  tests,  $n = 7$ ,  $p_s > .07$ ). Visits to other may be sampling behavior at most array spacings. This possibility is supported by the increased choice of other with spacing (Figure 2). If birds attended more to true spatial location as spacing increased, then they would be more aware that other flowers occurred at spatial locations they had never before visited. Such new flowers may be worth sampling. Our data cannot distinguish conclusively between the mistake and sampling hypotheses.

## Experiment 2

In Experiment 1, we presented hummingbirds with arrays of five visually identical flowers in which only the central flower contained the sucrose solution. When the array was shifted during a test trial, we found that the first flower the bird visited depended on the distance separating the flowers: The further apart they were, the less likely the bird was to choose the flower in the center of the array. Rather, the bird tended to choose the flower that occupied the same location in which the central flower had been previously. In Experiment 2, we again wished to determine the degree to which hummingbirds remembered rewarded flowers on the basis of absolute spatial cues versus relative or pattern cues. The task

was made more complicated by increasing the number of flowers in the array as well as by increasing the number of rewards to be remembered. The use of absolute versus relative spatial cues was further examined by making the flowers of some arrays visually identical and the flowers of others visually unique. We predicted that visual distinctiveness of the flowers should alter both the acquisition of the task (not studied in Experiment 1) and the salience of absolute versus relative spatial cues. We used only two levels of spacing within the arrays.

## Method

**Subjects.** Four experimentally naive, male rufous hummingbirds (*Selasphorus rufus*) were used as subjects in Experiment 2. As in Experiment 1, male hummingbirds were individually identifiable by marking their chests with a small amount of colored ink. Trials were run between 7:00 a.m. and 7:30 p.m. mountain standard time from May–July 1996.

**Initial training.** Artificial feeders containing 14% sucrose solution were placed in potential territories during mid-May, and by late May most feeders were defended by male hummingbirds. Four birds were trained to feed from small artificial flowers. These flowers consisted of a cardboard disk (5.8 cm in diameter), the center of which was pierced by a syringe tip forming a well capable of holding 120  $\mu$ l of sucrose solution. The cardboard disks were painted with unique and distinctive patterns with the use of 12 distinctive colors (red, green [dark and light], blue [dark and light], brown, white, yellow, orange, pink, purple, and peach; two colors per disc providing as high contrast as possible), providing visual cues based on both color and pattern. It is likely that the birds did not perceive the colors as we did, but we assumed that the variation in color and pattern meant the birds could discriminate among the variable flowers more easily than the flowers bearing the same color (and without pattern). The flowers were mounted on 60-cm wooden stakes. During training, the bird's feeder was removed, and the bird learned to feed from a single yellow flower containing 20% sucrose solution, which was moved a short distance (approximately 1 m) after each visit. When the bird had fed three times (less than 1 hr), the experiment began.

**Experimental protocol.** Sixteen flowers were laid out in a  $4 \times 4$  grid; 8 flowers contained 10- $\mu$ l 20% sucrose solution each, and the remaining 8 flowers contained water. There were four kinds of grids: (a) all 16 flowers the same color and pattern, 10 cm apart, center to center; (b) all 16 flowers the same color and pattern, 80 cm apart; (c) all 16 flowers different colors and patterns, 10 cm apart; (d) all 16 flowers different colors and patterns, 80 cm apart. There were four flower colors and patterns used for Grids A and B and 64 flowers used once on each of Grids C and D. For all of the grids, the flowers containing sucrose solution were in  $2 \times 2$  squares, arranged diagonally one from the other (see Figure 3). The bird was required to visit the grid and sample from the flowers until it had learned which of the 16 contained sucrose solution. A *visit* is defined as each occasion that the bird arrived at the array and attempted to feed from one or more flowers. Following each visit, the flowers the bird had drained were refilled with 10- $\mu$ l sucrose solution. The bird was considered to have learned the locations of the flowers containing sucrose solution when it had made three consecutive visits on which the percentage of rewarded flowers visited was 70% or greater. Immediately following this visit, a test trial occurred in which the grid was moved either 20 cm (Grids A and C) or 160 cm (Grids B and D) in one of the four main compass directions. This direction was pseudorandomly determined, as was the order of the grid presentation. When the bird returned to the

moved grid, all 16 flowers were empty, and the flower locations that the bird visited were recorded. Each bird completed 4 trials of each kind of grid, a total of 16 trials per bird. Birds experienced a mean of  $3.0 \pm 0.2$  test trials each day (range = 1–6 trials). ITIs (within-day, excluding between-day) averaged  $67.0 \pm 5.0$  min (range = 25–182 min).

**Results**

**Acquisition performance.** The number of trials the hummingbirds needed to learn the locations of the sucrose-rewarded flowers for the four different grids was assessed by use of a repeated measures analysis of variance (ANOVA). The first trial for each grid type for each bird was excluded from this analysis, as the birds all took at least this trial to learn to sample extensively within the grid (i.e., until some rewarded flowers were encountered). Birds never visited fewer than three flowers. Grid spacing had no effect on acquisition,  $F(1, 3) = 0.01, p > .90$ , but visual pattern did. Subjects learned the reward flowers more quickly when each flower was visually distinct than when they were all the same (Figure 4),  $F(1, 3) = 20.50, p = .02$ . There was no

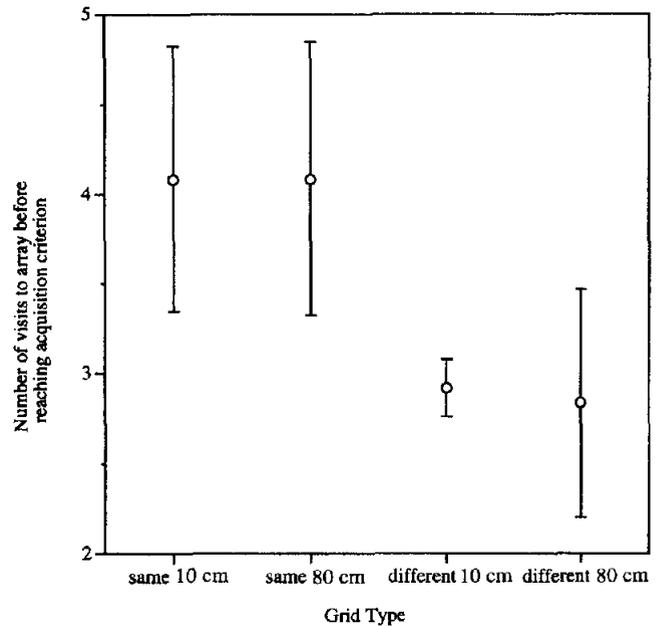


Figure 4. Number of trials before reaching the three criterion visits for each of the four birds. Values for all birds are combined for each of the grid types ( $\pm SE$ ).

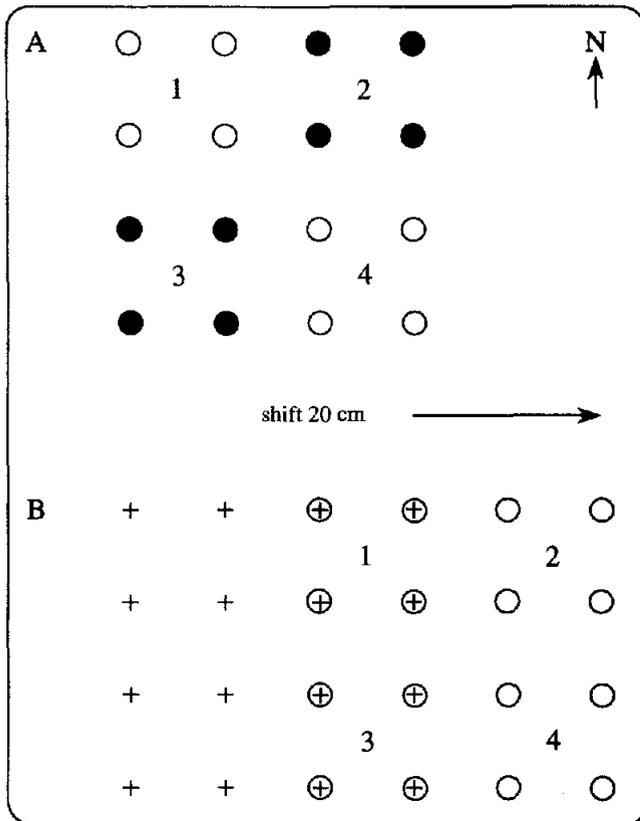


Figure 3. Schematic of the experimental design for Experiment 2. (A) Preshift; open circles represent unrewarded flowers, and solid circles represent sucrose-rewarded flowers. (B) Postshift; plus marks represent Preshift locations. No flowers were rewarded. Quadrants 2 and 3 represent the relative positions of preshift rewards. Quadrant 1 represents the actual spatial location of preshift rewards.

interaction between spacing and visual pattern,  $F(1, 3) = 0.01, p > .90$ .

**Experimental treatment.** The effect of moving the grid was assessed by a repeated measures ANOVA with three main effects: shift (preshift and postshift), pattern (same vs. different—unique visual appearance), and spacing (10 vs. 80 cm). The dependent measure was the percentage of correct performance defined as (a) the mean proportion of flowers visited that were rewarded in the preshift trials or (b) the mean proportion of flowers visited in the postshift trial that were in the relative position in the grid corresponding to reward flowers. There was no effect because of pattern or any of its interactions,  $F(1, 3) < 1.70, ps > .28$ . Both distance and shift showed main effects, but more important, their interaction was also significant,  $F(1, 3) = 26.70, p = .01$ . Preshift performance was high for both spacings, but postshift performance was significantly lower with the 80-cm spacing showing a greater decline than the 10-cm spacing (Figure 5). The average number of flowers visited on probe trials was  $8.5 \pm 0.4$  (range = 3–15 flowers).

If memory for reward flowers relied entirely on a perception of pattern within the array, then performance should have been maintained after the shift. These results suggest that subjects attended to spatial location to a sufficient degree and that postshift performance decreased significantly. To test more directly the possibility that subjects remembered the actual spatial locations of reward flowers, we examined postshift choices in detail. Following a shift, flowers could be classified in three different ways. Four flowers that had been unrewarded previously were shifted to

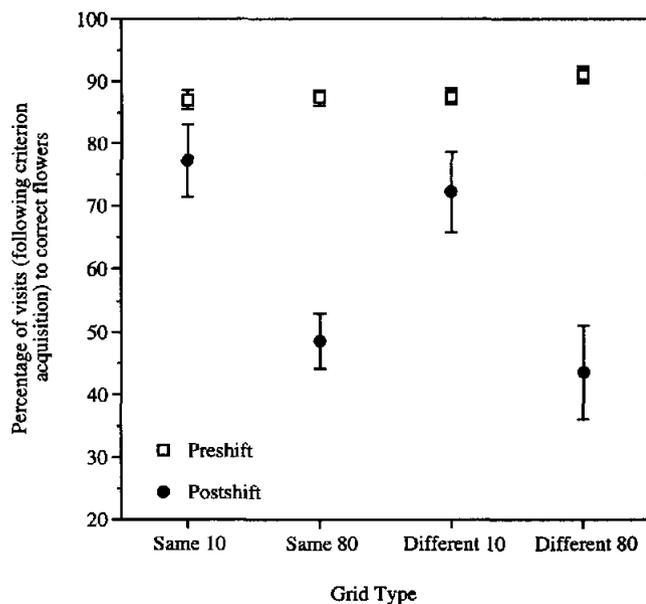


Figure 5. Percentage accuracy of locating the flowers containing sucrose solution before and after shifting the grid for each of the grid types (postshift flowers were all empty). Values are averages across birds with standard errors. Preshift performance is represented by open squares and postshift performance by filled circles.

entirely new locations (Quadrant 4 in Figure 3B); these are of no interest in this analysis. The other four flowers that had been unrewarded previously were shifted to spatial locations that had held rewarded flowers earlier. If subjects remembered actual spatial location they should have tended to visit these flowers (Quadrant 1 in Figure 3B). The other eight flowers were rewarded previously. If subjects remembered rewards according to their relative position within the grid (pattern), then they should have visited these flowers preferentially (Quadrants 2 and 3 in Figure 3B). We compared the mean proportion of the four location flowers chosen with the mean proportion of the eight position flowers chosen in a repeated measures ANOVA. The dependent variable was proportion of flowers chosen and the independent variables were choice (location vs. position), pattern (same vs. different), and spacing (10 vs. 80 cm).

The analyses revealed two significant interactions, both pertinent to our predictions. First, choice of location or position depended on spacing. At a spacing of 10 cm, subjects chose a greater proportion of the position flowers than location flowers, whereas at a spacing of 80 cm, subjects chose a greater proportion of location flowers than position flowers (Figure 6A),  $F(1, 3) = 2,143.90, p < .0001$ . Thus, the ways in which rewarded flowers were recalled depended on grid spacing.

The second interaction of interest concerns pattern and choice. When each flower was visually distinct, subjects visited similar proportions of location and position flowers. However, when the flowers were visually identical, subjects tended to visit more position flowers than location flowers (Figure 6B),  $F(1, 3) = 21.40, p = .02$ .

The only significant main effect was pattern,  $F(1, 3) = 14.30, p = .03$ . Subjects tended to visit more flowers when they were visually identical than when they were unique.

### General Discussion

The results from our experiments are as follows. In Experiment 1, the hummingbirds' choice of flower depended

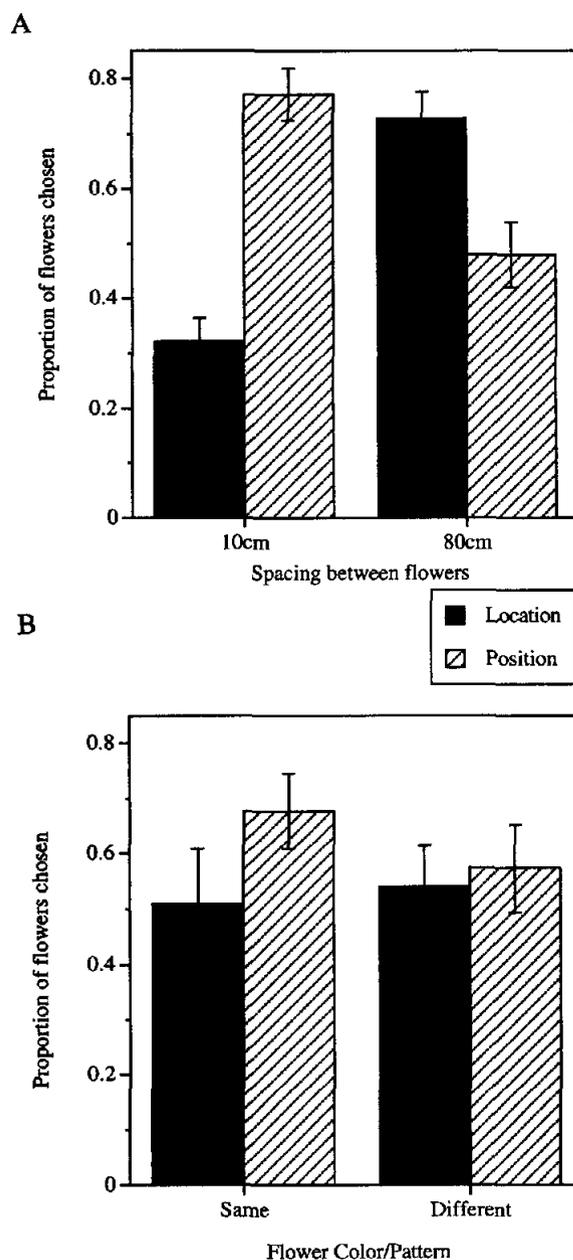


Figure 6. (A) The mean ( $\pm SE$ ) proportion of flowers in the appropriate position or location chosen, following the shift of the array for flower spacing of 10 cm and 80 cm. (B) The mean ( $\pm SE$ ) proportion of flowers in the appropriate position or location chosen, following the shift of the array for array with flowers of the same color and pattern or all flowers with different colors and patterns.

on the distance separating the flowers in the five-flower array. At distances of 40 cm or less, birds were most likely to visit the flower in the center of the array first (see Figure 2). When flowers were separated by more than 40 cm (up to 320 cm), birds were most likely to make their first visit to the flower occupying the previous location of the center rewarded flower. In Experiment 2, the birds learned the locations of the rewarded flowers in the array more quickly when the flowers had different color patterns, irrespective of the distance separating the flowers. However, when the array was moved and flowers no longer contained sucrose, the degree of disruption caused was most strongly correlated with the distance between flowers. When the flowers were 10 cm apart and the array was moved 20 cm, the birds' accuracy of locating previously rewarded flowers fell about 10%, regardless of the degree of similarity among flower color patterns. When the flowers in the array were 80 cm apart and moved 160 cm, the birds' accuracy of locating previously rewarded flowers fell to chance levels (50%), irrespective of flower similarity. All three predictions made prior to these experiments were supported or partially supported. (a) When flowers were closely spaced, birds tended to return to sites characterized by relative position, whereas when flowers were widely spaced they tended to return to sites characterized by absolute location. (b) When flowers were visually distinctive, birds showed no preference for flowers in the correct position or location, whereas when flowers were visually identical, birds tended to return to flowers in the correct relative position within the array. (c) Speed of acquisition was increased when the color and pattern of the flowers were unique, but spacing between flowers had no direct effect on acquisition rate.

The results from Experiment 1 seem to show that the birds used different cues to relocate the rewarded site and that the cues used depended on the spacing between the flowers in the array. When both the spacing and distance were small (40 cm or less), the birds chose to return to the site in the correct position relative to the other flowers in the array. We assume that returning to the site in the correct position involved the use of local, intra-array cues and that the birds returned to spatial locations by using extra-array cues.

The results from Experiment 2 show that memory for the multiple rewarded flowers was influenced by a number of factors. First, the color and pattern of the flowers influenced information acquisition. Rewarded flowers were learned more quickly when they were visually distinctive than when they were identical, and this effect was independent of spacing. Furthermore, birds attended more to relative position when flowers were visually identical. Second, attending to a flower's relative position also depended on the spacing between the flowers. At 10-cm spacings, birds tended to visit a greater proportion of flowers in the correct relative position, whereas at 80-cm spacings they tended to visit a greater proportion of flowers in the correct spatial location. Third, spatial location was always attended to as shown by the decline in performance following even small (20-cm) shifts of the array. Larger shifts had a more profound effect. These data are consistent with those from Experiment 1.

Preference for nearby local or intra-array cues, as seen in

our birds when flowers were close together, over larger, more conspicuous extra-array cues has been demonstrated in a number of studies (e.g., Bennett, 1993; Cheng, 1989; Collett, Cartwright, & Smith, 1986; Spetch, 1995; Spetch & Wilkie, 1994). As spacing between flowers increased in our experiments, flower choice changed, with birds apparently switching to the use of extra-array cues, whereas information provided by the arrangement of the flowers, color and pattern of the flowers, or both was seemingly ignored (e.g., Biegler & Morris, 1996; Margules & Gallistel, 1988; Olton & Samuelson, 1976). It is not clear what these extra-array cues were. They may have been plants and small bushes in the close vicinity of the array or even much larger objects several meters from the array (e.g., trees or the experimenter). As the distance of shift also increased with increased spacing, it is not clear whether the switch we see in flower choice is due to the spacing between flowers, the distance shifted, or both. Data from an experiment by Cheng (1988), in which he trained pigeons to find hidden food near an obvious landmark, offer support for the suggestion that the distance of shift is sufficient to have affected our hummingbirds' choice of flower. In Cheng's experiment, the pigeons' searching pattern shifted with the landmark when it was displaced with small distances, but, like our hummingbirds, the pigeons switched to the use of contextual cues to direct their searching as the local landmark was increasingly displaced.

One of the reasons for carrying out these experiments was to test explicitly whether rufous hummingbirds used a flower's relative position in some kind of spatial pattern during recall or whether they could, in fact, remember the spatial location of a flower. In the experiment carried out by Sutherland and Gass (1995), hummingbirds were tested on their ability to learn which 32 of 64 feeders contained sucrose solution. The feeders were closely spaced (11 cm apart) and were presented in a laboratory environment that was reasonably devoid of visual landmarks. Under these conditions, the birds appeared to use the relative position of feeders to return to correct locations, but the birds' potential ability to remember the actual location of feeders was not tested explicitly. Like Sutherland and Gass (1995), we found that rufous hummingbirds had a preference for returning to flowers in the appropriate position in the array when the spacings were small (up to 40 cm) but that this preference switched to one for the appropriate spatial location when distances increased. This switch may have been brought about, at least in part, by the rich diversity of visual landmarks available to our birds. We found that they were able to remember a flower's actual location and that this was most clearly observed when the flowers were separated by distances greater than 40 cm. It may be, then, that birds foraging on real flowers can remember both relative position of flowers, for example, when there are multiple flowers close together on the same plant, as well as actual location. The ability to remember actual locations would be useful for recording both the locations of plants bearing multiple flowers as well as the locations of flowers that occur singly.

Although the color and pattern of the flowers appeared to play little, or no, role in recall of the flowers' locations,

variation in color and pattern affected the rate at which the birds learned the locations of the rewarded flowers. The locations of rewarded flowers in an array were learned more rapidly when the flowers bore different colors and patterns from each other. This difference in speed of acquisition was not affected by the spacing between flowers. Sutherland and Gass (1995) found that speed of acquisition of a pattern of rewarded water-filled flowers increased as grain of pattern decreased, implying that the coarser grained patterns were somewhat easier to learn. A strategy of spatial chunking may explain this difference in ease of acquisition. We did not vary the grain of pattern in our experiment. An experiment that varied grain, spacing, and flower and color pattern and in which the order of flower visits was recorded might enable us to determine whether the birds do use a spatial-chunking strategy to learn locations, recall locations, or both, of flowers.

Although there was some variation in both acquisition and postshift performance among birds, all of the birds learned the rewarded locations after very few experiences and were affected in a similar fashion by shifting arrays. In these tests then, we found no evidence that there were differences among birds in memory capabilities or foraging technique (Valone, 1992).

Birds did not appear to approach the arrays from a consistent direction across trials, nor did they move around the flowers as if they were flying around a route. Further experimentation is required, however, to provide conclusive support for these observations. Previous experiments have shown that it is unlikely that the birds use olfactory cues from the flowers to determine whether or not the flower contains nectar and sucrose as honeybees do (von Frisch, 1967; Healy & Hurly, 1995; Hurly, 1996).

In summary, we found that rufous hummingbirds used the color and patterns of flowers to learn which flowers contained rewards but did not use these cues to recall locations of rewarded flowers. When the flowers were closely spaced (40 cm or less), the birds visited flowers in the correct relative position. When flowers were spaced at greater distances, however, birds visited flowers in the appropriate spatial locations. We attributed this change to the birds switching from the use of local, intra-array cues to global, extra-array cues when making choices about which flowers to visit.

We have shown previously that rufous hummingbirds prefer spatial over color and pattern cues, and those data are supported by the results presented here. It appears to matter little to the bird, having learned the location of a reward, that the rewarded location's visual aspects have changed dramatically (see also Carr & Watson, 1908; Lorenz, 1972). In our previous work (Hurly & Healy, 1996), we used an experimental design used by Brodbeck (1994), Brodbeck and Shettleworth (1995), and Clayton and Krebs (1994) to examine cue preference in food-storing songbirds. These studies showed that food storers had a much stronger preference for spatial cues over color cues. Nonstorers, on the other hand, did not show this striking preference. The rufous hummingbirds have a preference for spatial cues that is very similar to that of food storers (see also pigeons, Wilkie et al., 1985). In a

further experiment, Brodbeck (1994) moved his array of feeders in a fashion that resembles our array shifts, except that no feeder occupied that of another prior to the shift. Although it is not possible to determine how far apart feeders were in the first part of each trial, Brodbeck found that after shifting the array 89 cm, the black-capped chickadees' (*Parus atricapillus*, a food-storing species) ability to choose the feeder in the correct position in the array dropped to chance. Like our hummingbirds after such a shift of feeder array, Brodbeck's black-capped chickadees chose feeders according to their location in the aviary and only secondarily with respect to their color and pattern or array position. Brodbeck did not manipulate feeder visual cues in the ways we did (i.e., all of his were visually distinctive), so we cannot determine from his results how the chickadees used the different kinds of cues in acquisition. However, the chickadees did appear to take about twice as many trials to learn the location of the single-rewarded feeder than our birds did to learn the location of eight, even when all the flowers bore the same visual cue. Perhaps the abundant, natural, extramaze cues available to our birds enabled them to learn so quickly.

The very marked preference for spatial over visual cues shown by the hummingbirds may account for the following observations we have made on many occasions: A territorial male defending a feeder (large with a conspicuous red base) will return to this location even when the feeder has been removed. The bird appears not to register the feeder's absence until he fails to find it. This is true even when the feeder has been moved as short a distance as 30 cm, when the visual cues should still be in his field of vision. How the bird does not seem to see that the feeder is gone or has been moved is not clear. As the bird does not approach the feeder consistently from the same direction, it seems unlikely that this behavior is part of a straightforward, route-following strategy where the bird visits a number of food locations in a systematic path. The bird also cannot be using the feeder as a beacon. This behavior may mean that the animal does not update the local visual information until it is required to, that is, only when it discovers that the feeder is moved will the bird look for it. This lack of updating may be a way of reducing neural processing as it is either time-consuming or energetically costly. Alternatively, it may be that these hummingbirds are too busy looking out for competitors or potential mates. Support for this possibility comes from the observation that female and nonterritorial male hummingbirds do not seem to be unaware of a feeder's absence in the same way as territorial male hummingbirds are. Experimental testing is required to discriminate between these two possibilities.

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